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GYMNOSPERMS



PENHALLOW

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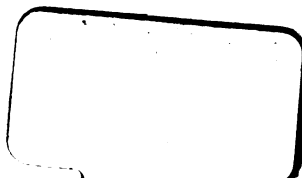


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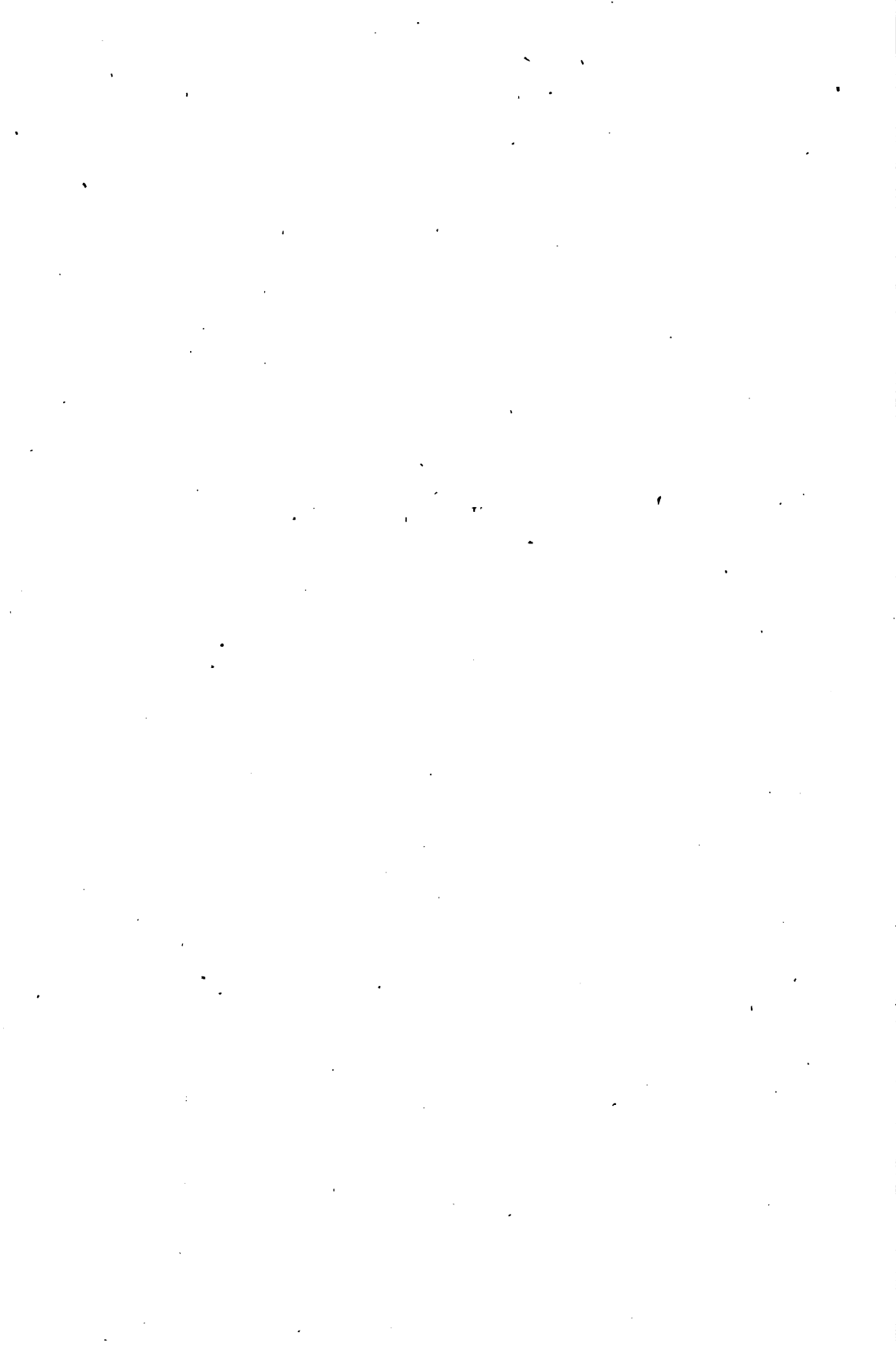
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# A MANUAL OF THE NORTH AMERICAN GYMNOSPERMS

EXCLUSIVE OF THE CYCADALES BUT  
TOGETHER WITH CERTAIN  
EXOTIC SPECIES

BY

DAVID PEARCE PENHALLOW, D.Sc.

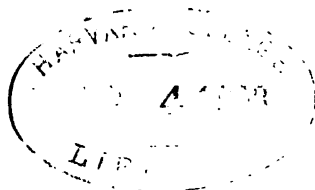
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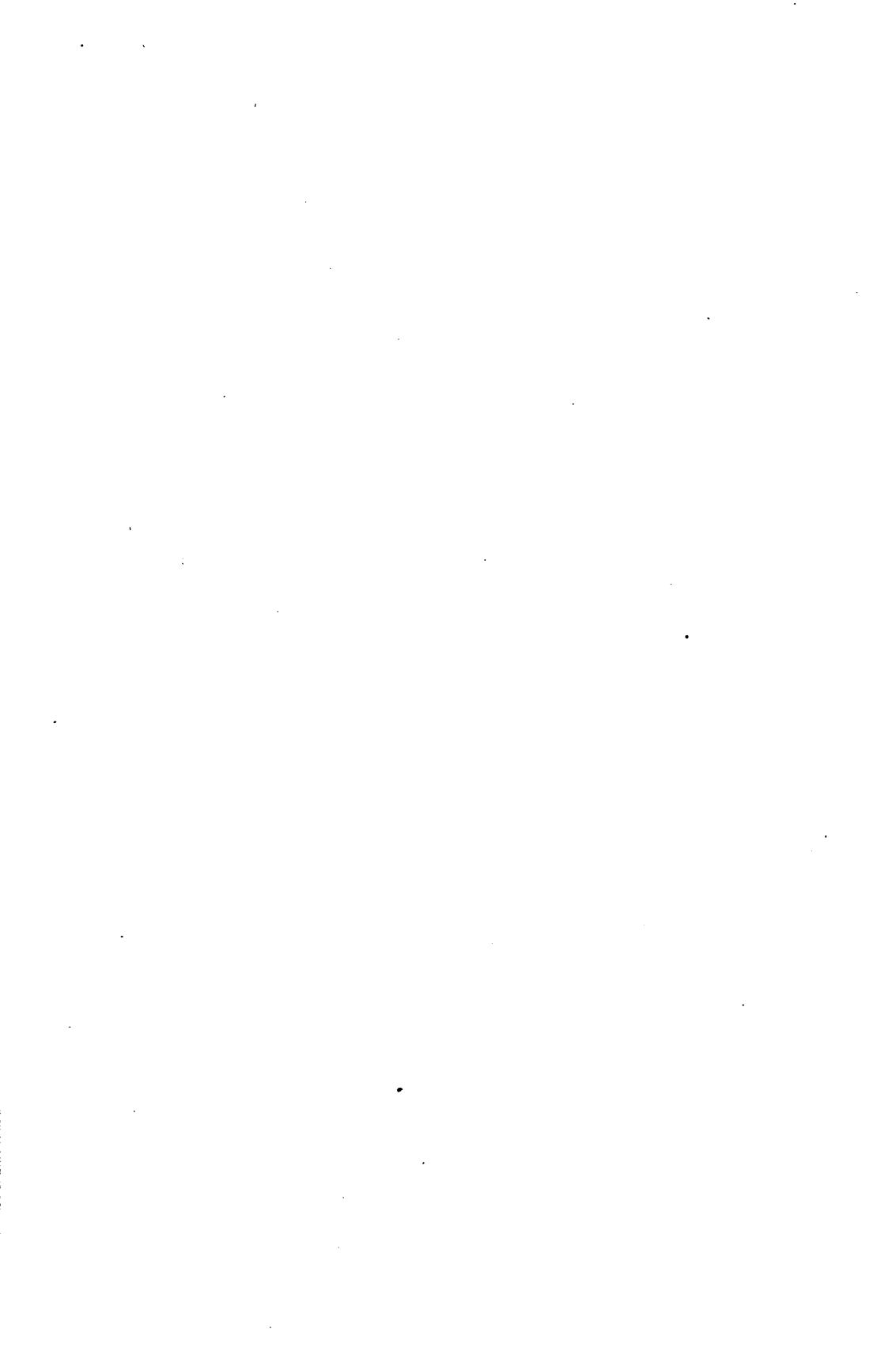
## PREFACE

In presenting this volume to working botanists the hope is indulged that it may also prove of service to engineers and especially to foresters. During its progress through the press various opportunities have been offered for testing not only the accuracy and value of the diagnoses for the recognition of woods about the identity of which there was some doubt, but also its general application to the elucidation of important questions relating to practical forestry; and the fact that such a work is greatly needed at this time, and may materially assist in the development of modern forestry, has been strongly emphasized. An important field for useful research may be found in an extension of the studies here indicated, not only with respect to exotic gymnosperms, but in their application to dicotyledonous woods, many of which present problems of great scientific interest and practical value.

An effort has been made to keep the work up to date, especially with respect to the treatment of fossil woods, but the author is only too conscious of many imperfections which it is hoped the application of the book to practical service may assist in making clear and ultimately removing.

D. P. PENHALLOW

MONTREAL, CANADA



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# **NORTH AMERICAN GYMNOSPERMS**

## **PART I—ANATOMY**



# PART I—ANATOMY

## INTRODUCTION

The present work had its origin in 1880, in an attempt to construct a system of classification for the North American Coniferæ based upon the anatomy of the vascular cylinder of the mature stem. The fundamental idea was that such a classification would prove of great value in the identification of material used for structural purposes, but investigations had not been carried very far when it became manifest that some such arrangement was imperatively demanded in other directions and for purposes of a more strictly scientific character. In entering upon the study of fossil plants it was recognized that the most fruitful source of reliable data must be found in the stem structure. At that time there was little in the way of an adequate basis for further study of this sort, inasmuch as the current diagnoses of the vascular structure were found in most cases to be singularly inadequate, and often so incorrect as to require extensive revisions. It was found furthermore that in order to reach correct conclusions in the case of stems which must often present marked structural alterations, arising through the influence of decay and other conditions attending fossilization in its various forms, it was indispensable that there should be a trustworthy means of comparison with existing types, whereby sources of error arising from eliminated structures might be definitely excluded, and the fossil referred with certainty to its nearest relative. The original intention was therefore modified with a view to meeting the requirements of paleobotanical research. During the time these investigations have been in progress there has been much change in the views held by botanists respecting the significance of anatomical features as affording evidence of descent; and our own



studies brought forth facts which gave repeated emphasis of the most positive kind to the idea that questions of phylogeny cannot be settled either by the morphologist in the narrower sense or by the physiologist when acting independently, and that a proper historical point of view can be gained only when to such labors we join the data derived from a critical study of the stem structure in all its details.

The original intention was to make a complete study of all the North American woods, comprising, as enumerated by Sargent in his report in the Tenth Census of the United States, some four hundred and nineteen species and varieties; but the great importance of the Coniferæ from an economic point of view, their frequent representation in the fossil state, and their relatively more simple structure eventually led to their selection as the one group in which initial studies might be prosecuted with the most immediate and profitable results. While the North American species constituted the original basis, various exotic species were added from time to time, with the result that our studies, as now completed, comprise ninety-two species from North America, twenty-one species from Japan, and four species from Australasia. This extension has proved of great value, not only from a paleontological point of view but also because of the important bearing such exotic types have had in the solution of questions relating to descent.

In determining the particular nature of the material to be dealt with in the prosecution of these studies several considerations of fundamental importance were kept in mind, among the more prominent of which we may consider the following.

The economic application of wood involves the employment, solely, of the material which lies within the woody zone between the bark and the pith. It was therefore held that for the recognition of timber or wood derived from constructions of any kind that these two latter regions of the stem would be worthless, and that a system should be devised which would, if possible, permit the recognition of the species apart from such structures. Experience has not only shown that this is possible, but that the characters

embodied in the structure of the pith and bark are, in most cases, least definite, and therefore of minimum value for differential purposes. Furthermore the structural variations which may be assumed to arise in conformity with the general evolution of the species or genus are always most pronounced in the xylem structure, in consequence of which the latter acquires exceptional value for purposes of relationship and phylogeny. Woody plants which are found in the fossil state often show a complete absence of pith structure, due to the operation of extended decay which may have been initiated before the tree or shrub ceased to live. Much more commonly fossil plants are devoid of bark. Instances are on record, as in the case of *Juniperus virginiana* from the Pleistocene clays, in which the plant is so perfectly and hermetically sealed up as to permit of a perfect preservation of the bark as well as of other portions of the stem, but such examples are comparatively rare. More commonly the extended maceration and decay to which plants are subjected before silicification or calcification occurs, involves a loosening and subsequent removal of the bark, especially when the tree is subjected to such mechanical action as is associated with its transport by water. It is therefore obvious that any system of classification which would serve the highest purposes for paleontological research must be wholly independent of both bark and the pith. Another consideration of importance in this connection relates to regional differences of such a nature that different parts of the stem exhibit more or less striking variations of structural detail. As these will be dealt with somewhat in detail in a subsequent chapter, it will be sufficient for the present purpose to indicate that the characters upon which the generic and specific differentiations rest are essentially independent of location, and it therefore matters not whether the sample selected comes from a branch or the main stem, or whether it is derived from the top, bottom, center, or circumference of the latter, though as a matter of preference the wood of a mature stem would be selected as furnishing the best average conditions of structure, and therefore the greatest facility in determination.

Two objects have been held in view in the preparation of this work : (1) its application to the needs of the scientific botanist in prosecuting researches either in recent or fossil forms, and (2) its adaptation to the requirements of the practical engineer who may be called upon to recognize material entering into the construction of bridges or other important works. While, therefore, Part I deals primarily with the anatomy of the stem, discussing such features as are essential to a correct knowledge and interpretation of the systematic portion, it also includes special chapters having a more or less direct bearing upon the practical utility of woods, — such as may be found in those on the general mode of operation of fungus parasites, the durability of woods under different conditions, and the specific action of decay upon the tissues. Owing to the great extent of ground covered by the subject of timber diseases and the special methods to be employed for their control, and the fact that an adequate discussion of these important topics would extend the present work much beyond all reasonable limits, the reader is referred for the treatment of diseases to Tubeuf (72), and for methods of wood preservation to important papers by Flad (20) and Constable (10). If such treatment of the general subject serves to secure a wider constituency among those who are called upon to make large use of valuable woods, one of the larger aims of the present work will have been achieved.

Part II is based upon the details of Part I, and it relates exclusively to questions of classification and relationship. In attempting to construct a classification of the Coniferales upon the basis of the anatomical characters to be found in the woody portion of the stem, it appeared that there was little to be obtained from the work of previous investigators which could be employed as a satisfactory working basis, since the results recorded by Nordlinger, Hartig, Muller, and others, while of great importance with respect to certain aspects of structure and affording many important suggestions, had not been carried to that point where they could be reduced to any very great practical utility. A survey of the literature of the subject showed that

the study of a particular group of woods was not sufficiently exhaustive to permit of final conclusions, and that in many cases the diagnoses were not drawn with sufficient attention to strict accuracy of statement and that regard for exhaustive detail which would render them of the greatest value. In dealing with the structure of the wood for taxonomic purposes it has been found that the diagnosis must take cognizance of a wide range of detail, and that it must be most searching in its character. This is a necessary result of the high degree of development of the organisms and the consequent differentiation of the structure along several lines of development. It is a neglect of this fact in the past which appears to explain why previous investigators have failed to construct a system of classification which would not only give some additional information respecting phylogeny, but which would at the same time permit of a satisfactory recognition of species and genera. Under these circumstances it appeared desirable to commence *de novo* and, in the first instance, make an exhaustive study of the anatomy of the wood, utilizing for purposes of classification such facts as might be obtained in this way. As a convenient starting point for the discussion of relationships it was considered that none could be secured which would be better adapted to the purpose in view than the classification generally employed as based upon the external morphology of the vegetative organs and inflorescence. For this purpose I at first selected the then most recent and authoritative compilation relating to the North American Coniferales, as embodied in Professor Sargent's valuable work on the woods of North America in the Tenth Census of the United States. To this were later added Sargent's *Silva of North America* and the sequence of Engler and Prantl contained in the *Natürlichen Pflanzenfamilien*, as expressing the latest views on the subject.

Assuming the typical character of the trees discussed by Sargent, it was held that any well-authenticated specimen of wood from any such tree would also be typical, and in this way it would be possible to form a type series the structure of which

could be discussed with direct reference to the assumed relationships based upon external characters. The nucleus of such a type series was found in the Sargent collection of woods derived from his work in connection with the Tenth Census. To this other specimens were added through the courtesy of Professor Sargent and Mr. J. G. Jack of the Arnold Arboretum; Dr. N. L. Britton of Columbia University, and now Director of the New York Botanical Garden; Mr. Morris K. Jesup, President of the American Museum of Natural History; and Dr. B. E. Fernow, then Chief Forester of the United States Department of Agriculture; also to the late Baron Ferdinand von Mueller of Melbourne, Australia; Sir W. T. Thiselton-Dyer, late Director of the Royal Gardens, Kew; Mr. E. J. Maxwell of Montreal; and more recently Dr. E. C. Jeffrey of Harvard University; to all of whom my grateful acknowledgments are due. Yet other specimens were obtained by personal collection or from trustworthy collectors whose reputation was sufficient guarantee for their authenticity. In this way it has been possible to include in the present list all of the North American species of the Coniferales as enumerated by Sargent in his *Silva*, with the exception of the recently described *Juniperus flaccida*. Present lack of material has also prevented me from making a critical study of *Juniperus barbadensis* in order to determine anatomically the identity which Sargent establishes on the basis of external characters; while the same conditions have also barred a study of *Juniperus scopulorum*, Sargent, and *Cupressus pygmæa*, Sargent, with a view to determining their validity as distinct species.

During the progress of the present studies a large amount of material came to hand from Japan and Australia. Its elaboration has afforded much information of the highest value, and it has been considered expedient to incorporate it in the present classification.

With this material in hand the first step was to secure an accurate diagnosis of each species for each of the three sections usual in such cases, and when it is recalled that, as at present elaborated, this involved a critical study of twenty genera and

one hundred and sixteen species, thus representing a total of three hundred and forty-eight sections, and that the diagnoses were at first of a purely tentative character demanding frequent revision and extension, it will be understood that the enormous mass of detail involved not only presented considerable difficulties but demanded the expenditure of much time and most patient and painstaking effort. The concurrent prosecution of paleontological studies, in which a very critical means of differentiation was called for, because of structural defects arising from decay and other influences attendant upon the process of fossilization, fortunately gave just the insight into the requirements of critical diagnoses which was required. It soon became clear that certain anatomical features stood forth with very great prominence, and that they could be successfully employed for the recognition of primary and secondary divisions of the group; while other less prominent characters naturally fell into the categories of those which define genera and species. Upon this basis it was soon possible to differentiate the various genera with accuracy, as already set forth in previous publications (44). The systematic treatment of the genera of the North American Coniferales then elaborated has been in constant and successful use for several years, as applied to the determination of both fossil and recent woods. Such experience has shown the classification to be substantially correct with respect to the accuracy of the diagnoses and the efficiency of the artificial key connected therewith. A few minor changes have been found necessary, and these have been introduced in connection with the more recent revisions. Later experience, especially as derived from a more critical study of the anatomical details, has shown the need of a revision of the generic and specific sequences, as embodied in recently published papers (59) and now incorporated here. As it now stands, comparatively slight familiarity with the classification will enable one to refer most woods to their appropriate genera without hesitation. Thus *Taxus*, *Torreya*, and *Pseudotsuga* may be isolated at once by the single character which they possess in common, — tracheids with spirals, — while the last

genus may be differentiated from the other two by the very simple, constant, and well-defined characteristics found in the presence of resin passages and fusiform rays. Yet once more, *Pseudotsuga*, *Larix*, *Picea*, and *Pinus* fall into a natural group characterized by the presence of resin passages, and within the group differentiation of the individual genera follows on natural and simple lines. This is particularly true of *Pseudotsuga* and *Pinus*, in each of which the generic characters are so well defined as to leave no room for doubt ; while yet once more, *Pinus* may be subdivided into well-defined groups, or subgenera, representative of the soft and hard pines. *Abies* and *Tsuga* are differentiated by the position of the resin cells and the character of the terminal walls of the ray cells ; *Sequoia* and *Taxodium* are separated by the terminal walls of the ray cells, the character of the bordered pits on the lateral walls of the ray cells, and by the distribution of the resin cells ; *Cupressus* and *Thuja* are differentiated by the terminal walls of the ray cells, the distribution of the resin cells, the form of the pits on the lateral walls of the ray cells, and the form of the ray cells in tangential section. These principles are applicable to all other genera, and the key as now presented affords a trustworthy guide.

For the species the question has been found to involve much greater difficulties, especially with reference to the genus *Pinus*, in which the number of essential elements increases greatly, while extreme variation also introduces a factor which adds much to the complexity of the problem. Two sources of error were early recognized as probable, — (1) incorrectly drawn or incomplete diagnoses, and (2) deviation from the selected type. The problem was to elaborate an analytical key of such completeness as to eliminate any such errors, and then apply to it a test which would prove the extent of its accuracy, employing the data so obtained in further corrections if necessary. For the purposes of a critical test I was furnished with carefully selected material by Mr. Jack and Dr. Fernow to the extent of eighty-five specimens representative of fourteen genera and forty-nine species. The specimens received from Mr. Jack

represented a great variety of material in common use for structural purposes. They included wood not only from the mature parts of the stem but also from the center of the trunk, embracing in some instances the structure of the pith and primary wood zone. For these reasons they possessed special value, inasmuch as they afforded an opportunity to determine the extent and nature of those structural variations which I had some reason to believe existed, as between the earlier and later growths of the stem. In transmitting his material Dr. Fernow stated that he had selected it "with reference to representing typical wood, and it was not taken from butt logs, top logs, nor branches or knots." It therefore represented exactly the problems which would be met with in every-day practice.

The results of these tests as at first obtained were far from satisfactory. They clearly proved that the genera could be recognized with ease, but for the species they made it clear that there was need for a far more detailed diagnosis and differential key than was at first supposed to be necessary. More searching studies were made not only with respect to existing types but also as applied to fossil species from the Devonian to the Interglacial. These studies necessitated frequent recastings of diagnoses and corresponding alterations of the analytical key. They brought to light many important facts and relationships of the greatest value from a phylogenetic point of view as well as from the taxonomic, and they served to emphasize the fact that many of the more detailed structural features of the pines in particular, hitherto supposed to be of little or no value, were in reality of the greatest importance. A final application of the test specimens under the precise conditions which would obtain in ordinary practice showed a verification of 91.5 per cent for all genera and species. In this connection it may be of interest to note that the greatest sources of error were to be found in the second section of the genus *Pinus*, particularly in *P. taeda*, *P. echinata*, and *P. glabra* in the order given, whence it appears that these species stand out as the most variable of the entire Coniferales and, on the whole, the most difficult to determine. This is in precise accord with the



fact that these species are among the most highly specialized representatives of the entire phylum, and that they therefore stand as representatives of the highest order of development. The sources of error having been determined by such tests, corrections were applied to the key in such a way as to eliminate them, while the original diagnoses were further modified to meet the special requirements. It is manifestly impossible to construct a key capable of providing for all exceptional cases. These can only be met by the experience of the observer or by final reference to and critical comparison with type specimens. But the experience so far gained justifies the belief that as now presented the key affords sufficient data for the recognition of species under all ordinary circumstances, and there is no reason for hesitation in stating that it is fully as efficient in this respect as the keys usually employed for the determination of species on the basis of external morphology.

In the employment of this classification the novice will encounter certain practical difficulties the nature of some of which it may be well to indicate. In the genus *Picea* the differentiation of species is attended with more than the usual difficulty, and the same fact appears once more in the second division of the genus *Pinus*. This appears to be the result of a general advance toward a higher type of development, in consequence of which there is a more uniform distribution of similar characters among the various species. This feature also appears occasionally in other genera, especially in *Juniperus*, where it is not altogether easy to differentiate *J. nana* from *J. communis*, of which it has commonly been regarded as a varietal form. But *J. rigida* shows precisely the same relations to both of these, and I therefore prefer to retain the specific status of all three, though somewhat provisionally. In *Pseudotsuga* there is as much anatomical difference between *P. Douglasii* and *P. macrocarpa* as there is between any well-known and well-recognized species. There is therefore no reason for assigning the latter to a varietal position, and it should be given the status of a species, as correctly suggested by Sargent. In the genus *Pinus*, *P. Murrayana* cannot be regarded

as anatomically identical with *P. contorta*, as suggested by Sargent, for the same reasons as already applied to *Pseudotsuga*. Similarly *P. Jeffreyi* is a valid species and *P. ponderosa scopulorum* must be raised to the position of a species, while yet others fall into the same category.

The sequence of genera and species, as well as the relations of the larger groups, is based upon the anatomical data presented in Part I, and it will be found to deviate considerably from most of the systems of classification now in use. In exhibiting this sequence, which appears abundantly justified from one point of view, it must nevertheless be carefully kept in mind that such an arrangement is in no sense regarded as final. At best it is a purely tentative measure, which shall serve as a contribution toward a final classification, and this latter can be completed only when data from several sources are assembled and coordinated.

As derived from our present studies the sequence of the Gymnosperms may be stated as in table on the following page.

With respect to fossil forms an effort has been made to include all known North American species so far as they have been recognized through the structure of the wood alone. These have been included under their respective genera as now known for existing species, and thus *Cupressinoxylon*<sup>1</sup> or *Cupressoxygen* are described under *Cupressus*, while *Pinoxylon* and *Pityoxylon* fall under *Pinus*. Unfortunately, in most cases, it is not possible to determine the structural characters with that detailed thoroughness which is desirable, owing to the imperfect nature of the material, and it has therefore been found necessary to arrange the fossil species in a separate section of the genus and provide separate analytical keys. The very great difficulty of obtaining full differential characters necessitates reference to type specimens whenever a serious doubt arises. In several cases the

<sup>1</sup> The genus *Cupressinoxylon*, as elsewhere shown, embraces what may prove upon revision of existing descriptions *Sequoia* in some cases and *Cupressus* in other cases, while according to Jeffrey's latest publications he employs the term for fossil *Sequoias*. Provisionally I prefer to include it under the genus *Cupressus*.

## CLASS I. CYCADALES.

## II. CORDAITALES.

## Order 1. Cordaitæ.

## Family 1. Cordaitaceæ.

## Genus 1. Cordaites.

## 2. Araucariineæ.

## 2. Araucariæ.

## 1. Dammara.

## 2. Araucaria.

## III. GINGKOALES.

## 3. Gingkoineæ.

## 3. Gingkoaceæ.

## 1. Gingko.

## IV. CONIFERALES.

## 4. Taxoideæ.

## 4. Taxaceæ.

## 1. Torreya.

## 2. Taxus.

## 5. Podocarpaceæ.

## 1. Podocarpus.

## 5. Coniferæ.

## 6. Taxodiineæ.

## 1. Cryptomeria.

## 2. Taxodium.

## 3. Sequoia.

## 7. Cupressineæ.

## 1. Thujopsis.

## 2. Libocedrus.

## 3. Thuya.

## 4. Cupressus.

## 5. Juniperus.

## 8. Abietineæ.

## 1. Abies.

## 2. Tsuga.

## 3. Pseudotsuga.

## 4. Larix.

## 5. Picea.

## 9. Pinoideæ.

## 1. Pinus.

diagnoses are given provisionally, since it is quite probable that in consequence of the fragmentary nature of the available material future studies will show several supposed species to be really identical with one another. In the case of a large number of fossil species it has not been found possible to obtain the type sections for descriptive purposes. Under these circumstances, although the original diagnoses differ materially from the general plan adopted, it has been thought best to incorporate them in the form of first publication, but with the name of the author appended.

All of the illustrations employed in the preparation of the present work have been prepared from drawings and photographs by the author, and they may therefore be regarded as being particularly applicable to the various questions brought under discussion. Nearly all the text figures were first published in the *American Naturalist*, and are here reproduced through the courtesy of that journal. Some of the half-tone reproductions of photomicrographs appeared in earlier papers relating to fossil and recent gymnosperms, while yet others are introduced here for the first time. It has been impossible to introduce all the illustrations which the clearest exposition might make desirable, owing to the limitations imposed by the expense of such a proceeding; but it is felt that the very generous allowance made by the publishers in this respect will suffice to render the leading facts of structure and relationship clear enough for our present purpose.

## CHAPTER I

### GENERAL DIRECTIONS AS TO THE PREPARATION OF MATERIAL AND THE VALUE OF PARTICULAR SECTIONS

In determining the course to be followed in the preparation of material and its subsequent study, it is impossible to too strongly emphasize the fact that a correct and complete conception of the details of structure embraced in the vascular cylinder of the stem can be obtained only when the latter is studied from three points of view, or in three planes of section, — the transverse, the radial, and the tangential, the last two of which are of necessity also longitudinal. Although the importance of these three planes of section is well recognized by scientific botanists, it seems desirable to restate the fact in order to avoid any misconception which might otherwise arise through the minor importance attached to the longitudinal sections by recent authors (79, 350). Under certain circumstances it sometimes happens that all three planes of section are not available, and the student is then compelled to rely upon two points of view or possibly even one for his conclusions. In such an extremity it becomes possible to draw deductions from the material in hand as to the aspects of the structure presented by the remaining plane or planes of section, and so to reconstruct with approximate accuracy the entire fabric. But such a method should never be resorted to except when absolutely necessary, since to employ it under other circumstances would involve a measure of doubt which would bring justifiable discredit upon the conclusions reached. The relative value of each section for such purposes will appear shortly.

In proceeding to the study of a given wood too much stress cannot be placed upon the importance of very searching and accurate observations, especially if one is about to draw a diagnosis

of a new species. In making a diagnosis for comparison with that of a previously described species similar care is a necessity, particularly in the case of the different hard pines, where a comparatively slight deviation may involve one in considerable difficulty. Until one is thoroughly familiar with the course of procedure to be followed, and has an extensive knowledge of the anatomical details in all their varying aspects as characteristic of different genera and species, the only safe course to follow, when attempting to identify a species, is to make a carefully written diagnosis in full. After this is done comparison with the key or with the supposed species may be made in detail. A comparatively brief acquaintance with the systematic portion of this work will enable one to recognize most of the genera at sight, since the characters are in most cases very clearly defined and easy of recognition; but the same does not hold true of species, since these are defined by a larger number of characters which vary somewhat widely, and exceptional cases are of much greater frequency. Where there is a final doubt as to the identity of a given species, the specimen should be compared with a type section or be submitted to an expert for decision.

*The transverse section* exhibits in the main an end view of the various component elements. It should always be the first of the three to be examined, since it immediately permits a separation of the genera into two great groups and affords suggestions of such a nature as to permit of economy of time at a later stage of the examination. It conveys a correct conception of the presence or absence of certain structural features, such as resin passages, resin cells, or resin cysts and the presence or absence of thyloses; it affords the only accurate measure of regional distribution and of the general character of the growth rings, the relative volume and character of the spring and summer woods, and of the variations which distinguish the tracheids of those regions of growth. When elements have similar terminal aspects, as the spiral and pitted tracheids, as well as wood parenchyma and parenchyma tracheids, the transverse section has no special value beyond that which is to be found in a recognition of

regional distribution, although to a limited extent it is true that certain aspects of these elements may lead to correct inferences as to their structural features when displayed in other planes of section, whereby approximately correct data may be obtained even in the absence of longitudinal sections. This is particularly true with respect to the distribution of the resin passages, the relations of their longitudinal and radial distribution being such that where the one occurs the other may be inferred; hence, if resin passages occur in the transverse section, we may conclude with certainty that they are also to be found in certain of the medullary rays, which will also present a fusiform aspect in tangential section.<sup>1</sup> The general character of the medullary ray is also displayed in this plane of section, but in its least important aspect. Although all the details of width and composition may be obtained much more accurately, and in some cases only from longitudinal sections, nevertheless the absence of these latter enables us to determine from the transverse section whether the rays are one or more seriate and if some of them contain resin passages.

In order that the features thus indicated may be exhibited in their typical aspects, it is of the greatest importance that the plane of section be exactly at right angles to the axis of growth, otherwise the distortion of structure which necessarily results will not only make observation difficult, but it will serve to seriously impair the accuracy and value of any diagnosis which may be drawn.

*The radial section* is also a longitudinal section the plane of which should exactly coincide with the radius of the stem. Any deviation from this position will cause the section to become more or less tangential, and just in proportion as it approaches this latter will its value diminish. In stems or branches more than five centimeters in diameter there should not be the least difficulty in securing the desired result, inasmuch as the abundance of material will admit of somewhat reckless cutting; but in small branches of one centimeter or less, such as one must

<sup>1</sup> Certain exceptions to this law are to be met with in the case of fossil species.

encounter in the case of fossil material, great care should be exercised in order to secure the few truly radial sections which the scanty material affords. When properly prepared such radial sections supply some of the most important data for diagnostic purposes. They furnish but little information as to regional distribution, a feature which is of secondary importance in this case. They do, however, furnish evidence of the highest value as to the form and structure of the tracheids, the character and extent of the transition zone, the regional distribution of the bordered pits and the various important details of their structure, size, and aggregation, the disposition and character of the spirals, and, above all, it gives the only adequate knowledge of the medullary ray with respect to those features which are of the greatest value in the final differentiation of species. It is true that some of the features of the ray may be inferred from a transverse and more particularly from a tangential section, but they cannot be utilized fully except in generic differentiations. The radial section gives a complete side view of the ray, exposing the entire structure in all its details throughout the whole radial extent. It is from such data that we obtain our final decision respecting the separation of the first and second sections of the genus *Pinus*, the differentiation of *Sequoia*, *Libocedrus*, and *Taxodium*, the recognition of species wherever found, a differentiation of the *Taxodiineæ* from the *Cupressineæ*; and since it exposes the entire structure in all its details, which are presented chiefly in side view, it permits us to determine their relations to one another and to the activities of the plant as no other section can. As features of subordinate value the radial section completes our knowledge of the bordered pit, which it presents in section wherever these structures lie in the tangential walls, a distribution which may be more accurately ascertained in this plane of section than in the tangential, since they are more certain to occur within the limits of a given field. For similar reasons the radial section affords the most convenient means of studying the longitudinal aspects of resin passages, resin cysts, resin cells, and crystallogenous idioblasts.



*The tangential section*, which is also a longitudinal one, is such as cuts a given radius at right angles, and it is most completely such in all its parts when none of the included medullary rays are cut diagonally. This result is always possible in stems of large size from which typical tangential sections of several square centimeters may be cut without difficulty; but in small stems it often happens that only one or two sections of value can be obtained, since the nearer the plane of section approaches the center of the stem the more nearly does it approximate to a radial section. It follows from this that in many cases sections will have to be employed in which only a limited area exposes the typical structure, all the rest being partially radial. With respect to the latter it should be pointed out that any deviation from a strictly tangential plane will involve a distortion of the structure of the medullary ray, and inasmuch as the value of the latter for diagnostic purposes rests very largely upon the form of the ray cells, it will be evident that even a slight reduction of the angle from ninety degrees must introduce an alteration of form which renders the ray of no value. The chief value of the tangential section is thus seen to lie in its exposure of the extremities of the rays, the general composition and number of which may then be ascertained with accuracy. From this it is possible to infer the presence of certain structures in the transverse section, such as the resin passages, since as already pointed out there are very constant relations between the occurrence of such passages in the rays and in the longitudinal structure. Important exceptions to this otherwise general law are to be met with in certain resin cysts of traumatic origin among recent plants, and also in the case of certain extinct species. Thus *Sequoia Burgessii* does not exhibit resin passages in a transverse section, though they do occur and are characteristically developed in the medullary rays. Precisely similar structural conditions are to be found in *Pityoxylon chasense*. From the recent studies of Jeffrey, however (25), we are led to the inference that such unusual relations, which at first seem to indicate some peculiar feature in development, may in reality be due to the fact that the longitudinal resin

passages occur at such wide intervals, or are so grouped within narrow areas, that a given specimen may show none of them in transverse section, although a very considerable area is examined. In a minor degree the tangential section is also useful but not necessary in extending our knowledge respecting the distribution of bordered pits in the tangential walls of the tracheids, but whenever such features are to be studied critically it will be necessary to provide two tangential sections for each species, one passing through the spring wood and the other through the summer wood.

For the preparation of sections of fossil woods which are strongly silicified or calcified, or otherwise infiltrated with mineral matter, special apparatus for cutting and grinding is required, and this part of the work is best accomplished by intrusting it to one who has gained the necessary dexterity through long experience. For those fossil woods of comparatively recent deposits, such as the Pleistocene or later formations, which have undergone little or no modification by the infiltration of mineral matter, the methods applicable to woods from existing species will be found to meet all the requirements of the case. Where there has been a slight infiltration of mineral matter, boiling with sodium carbonate will in most cases serve to remove the carbonate or silicate, as the case may be, and bring the material into such condition that it may be cut with facility by the microtome knife. In all such cases, however, before mounting for examination, care must be taken to fully neutralize the action of the alkali by the action of dilute acetic acid, which serves to restore the structure to its normal volume.

In the case of recent coniferous woods it will meet all the requirements of the case and amply provide for species determinations if blocks about one centimeter cube are boiled in water from one half to two or three hours and then sectioned while hot. The sections should be cut as thin as possible, carefully freed from air, stained, and mounted in Canada balsam. In thickness the sections should be as nearly as possible of the diameter of a tracheid or less, and this may be accomplished by means of a

carefully sharpened plane, which is, in some respects, one of the very best of section cutters where the work does not call for the most critical methods. Preferably the blocks which have been boiled as described may be sectioned on a microtome in the usual way. For this purpose any instrument which provides a high degree of rigidity may be employed.<sup>1</sup> For purposes of very exact study more elaborate methods and more expensive instruments will have to be employed, but since these relate chiefly to botanical laboratories where they are already well known, they need not be specified here.

For the purpose of freeing the sections from air, a somewhat troublesome process where sections are prepared as specified, the air pump may be used; but a far more simple and less costly method is to boil the sections in water for five or ten minutes and then plunge them directly into 95 per cent alcohol. At intervals of five minutes or so alternate the treatment with alcohol and water, and, except in some of the most troublesome woods, such as the spruces and larches, it will be found that the air is all discharged in the course of half an hour. As a matter of precaution the sections should then be left over night in 95 per cent alcohol in order to secure complete dehydration.

Before mounting in balsam the sections must be stained. For this purpose almost any of the well-known aniline stains or Delafield's hematoxylin may be employed, the object being to secure a perfectly sharp and well-defined image on a clear field. But in the study of woods it is often of importance to be able to photograph what is seen, and as all the stains are not equally valuable for this purpose the dye should be selected with special reference to the results sought. Where instantaneous exposures are to be employed nothing is better than Delafield's hematoxylin, which is allowed to act until a deep purple color is produced. But this stain will not answer for time exposures as well

<sup>1</sup> One of the best of simple instruments is the table microtome made by Bausch and Lomb, but the knife used with this form of instrument should be a plane blade mounted in a heavy wooden handle of such form as to secure a perfectly firm grip.

as some others. Under these requirements we may employ a strong alcoholic solution of Bismarck brown which is actinically opaque. By its use walls which are presented in section do not transmit enough light to affect the plate even after rather long exposures, while those walls which are presented in side view and are relatively of little volume transmit enough light to make a strong contrast. By using such process plates as the Imperial a well-taken negative will show sharply contrasting black and white and will bring out all the details. All of the photographs in the present work were taken in this way.

After staining the sections should be passed into oil of cloves until thoroughly cleared, after which they should be mounted in xylol balsam.

## CHAPTER II

### THE GROWTH RING

In proceeding to a study of the transverse section the first feature to which attention is naturally directed is the *growth ring*. These are either *broad* or *narrow*, *variable* or *uniform*, *eccentric* or *regularly concentric* according to their relative proportions in radial extent, the constancy of their radial volume, and their equal or unequal development at all points about a common center. While a recognition of such features often serves an important purpose in confirming data from other sources, they are in reality of secondary importance and too much stress must not be laid upon them; in fact, they may, if necessary, be entirely neglected in most cases. This element of doubt is due to the fact that within a given transverse section of an entire stem the growth rings vary very greatly among themselves as the result of varying rates of growth induced by external conditions of soil and climate. These variations are of such a nature that, in general terms, the growth rings will have the greatest radial dimension in a young stem or at the top or toward the center of an old stem, while such dimension diminishes within the same stem radially outward, so that in the peripheral portion of a very old trunk the rings will be either actually or relatively very narrow. This general rule is subject to many exceptions. In consequence of the suggestions furnished by this structural feature it is desirable to include its description in every diagnosis of a species, and we may therefore consider somewhat in detail its principal aspects of structure and variation.

All of the North American Coniferales without exception, both fossil and recent, and also all of the Japanese species so far investigated, are characterized by well-defined growth rings. These regularly recurring zones of growth, arising through

alternating periods of physiological rest and activity, correspond very closely with annual periods, whence it is possible to utilize them in determining questions of age which may be ascertained in northern latitudes within an error not exceeding and usually much less than one per cent (53, 162). This law has been applied with success to the determination of the probable age of certain blazes found in beech trees in Canada, tracing them to the year 1721 and their probable origin at the hands of some of the early Franciscan missionaries (54, 356, and 55, 500); while Campbell has similarly applied it to a determination of the age of certain Sequoias and the years in which forest fires or other injuries were inflicted (9, 335). The chief sources of error in such estimates lie in the difficulty of clearly recognizing under all conditions the relation of a particular growth ring to a certain year, since it is a well-known fact that under peculiar conditions more than one ring may be formed in one season. Thus Penhallow has shown that while in northern latitudes there is an essential constancy in the relation of rings to annual periods, this constancy diminishes toward the equator with a tendency to the obliteration of the growth rings, whence it follows that at some intermediate point in latitude there will be more rings formed within a given period than there are years of age (53, 162). This is supported by the observed fact that in the state of New York the common red maple (*Acer rubrum*) has been known to form an average of three rings for each year of growth, while in Florida at least forty rings have been found in trees less than thirty years old. In such cases experience will soon indicate to the observer that the demarcation between rings of successive years is much more pronounced than between those of the same year, directly corresponding to the duration and intensity of the rest periods in each case, and from this it is possible to reduce the error from such a source to a minimum. Thus De Bary has shown that such double growth rings as are referred to are the direct result of some disturbance of the normal course of growth for the season, such as may arise through the operation of frost, drought, insects, etc. (13, 514).

A concrete illustration of the conditions which would be likely to produce such a result is presented in a late frost which seriously affected vegetation in the neighborhood of Montreal in the spring of 1902. On the 9th and 10th of May of that year a cold wave passed over Montreal, and inflicted such serious losses upon early crops and effected so much damage to trees and shrubs as to excite much comment. At that time nearly all trees and shrubs were in tender leaf. Many were either in bloom or the flower buds—as in the horse-chestnut—were well formed but not open. In such cases the new branches had already attained a considerable length, but in many of the later species, such as Catalpa, the English maple (*Acer campestre*), sumac (*Rhus typhina*), and the ash, the leaf buds were not opened and no material injury resulted. In all of the earlier forms, however, the leaves and young branches were killed, and in the horse-chestnut and elder (*Sambucus racemosa*) recovery involved the formation of an entirely new set of organs from latent or adventitious buds. In such cases it is altogether likely that an examination of the wood for that year would show two rings of growth, between which the distinction might be expected to be less clearly defined than between those of successive years.

Variations in the width and prominence of growth rings of successive years are in some cases so marked that, were pieces of wood from the same stem to be examined without any knowledge of their previous relations, they might be regarded as representing wholly different species. This is notably the case in the hard pines, such as *P. palustris*, *P. cubensis*, *P. echinata*, etc., while it is also true of *Pseudotsuga Douglasii*, in which this feature has been critically studied. In a large cross section of this wood, embracing five hundred and thirty-eight growth rings, the latter were found to be disposed in well-defined zones, which vary greatly in width, while the component rings of contiguous zones show well-marked differences in radial volume. An instructive example of such growth is given by Hartig (22, 40) in the case of the Tyrolean larch, taken from a height of a thousand meters and having an age of one hundred and ninety years

though only nineteen centimeters in diameter. Further, within each zone (*Pseudotsuga*) the range of variation is narrower, and oftentimes the rings present a remarkable degree of uniformity. So well marked are these differences that when a number of trees are examined it is possible to establish an exact correspondence of zones by means of the average dimensions of the component growth rings. These facts point with some force to the probable operation of similar, if not identical, conditions of growth over a somewhat extended period, while the periodicity of growth also suggests a corresponding periodicity in environmental conditions. It has elsewhere been shown (52, 35) that in the case of trees exhibiting four such zones the following results are obtainable :

VARIATIONS OF ZONES AND GROWTH RINGS IN  
PSEUDOTSUGA DOUGLASII

		ZONE 1	ZONE 2	ZONE 3	ZONE 4
No. 35	Total width of zone, cm. . . .	2.12	15.77	16.48	0.00
	Number of rings . . . . .	5	73	141	0
	Average width of rings, mm. .	4.24	2.16	1.17	0.00
No. 2	Total width of zone, cm. . . .	0.00	11.95	4.52	0.00
	Number of rings . . . . .	0	50	38	0
	Average width of rings, mm. .	0.00	2.38	1.19	0.00
No. 789	Total width of zone, cm. . . .	17.07	2.85	4.77	1.36
	Number of rings . . . . .	39	10	27	14
	Average width of rings, mm. .	4.38	2.85	1.70	0.97
No. 428	Total width of zone, cm. . . .	2.72	16.38	0.70	0.00
	Number of rings . . . . .	8	66	4	0
	Average width of rings, mm. .	3.40	2.52	1.75	0.00
No. 316	Total width of zone, cm. . . .	16.28	4.42	3.23	0.85
	Number of rings . . . . .	33	17	28	10
	Average width of rings, mm. .	4.96	2.60	1.15	0.85
	Totals, mm. . . . .	16.95	12.51	6.96	1.82
	Averages, mm. . . . .	4.24	2.50	1.39	0.91



The variations thus indicated are usually accompanied by a more or less marked alteration in the relative volumes of the spring and summer woods, in consequence of which the same tree may show regions of coarse-grained and fine-grained wood. Plate 1 exhibits the characteristic features of such fine-grained wood, and a comparison with plate 46 will serve to emphasize the deviation from the usual type of structure.

Eccentricity of the growth ring is a feature more or less common to all woods (31, 513), and it is determined by external conditions of light and warmth (22, 41 *et seq.*), but ordinarily such variations are not sufficiently marked to merit comment. In the genus *Juniperus*, however, eccentricity is developed to an unusual extent, and it serves as a more or less distinguishing feature. From the photograph presented in plate 2 it will be seen that the rings not infrequently coalesce on one side, while gaining great prominence as separate structures on the opposite side. A like eccentricity characterizes the genus *Taxus*.

We are then to conclude that growth rings are a normal and constant feature in the stem structure of the Coniferales as a whole, and the same is also true of the Ginkgoales so far as we know them through both fossil and recent examples of the genus *Ginkgo*. But the same law does not apply to the Cordaitales as a whole, and in this may be found one of the leading distinctions between these two groups. This is especially true of the genus *Cordaite* in which the "growth rings when present are obscure, rarely somewhat conspicuous," and even in the latter case they appear simply as regions of somewhat unequally variable density, dependent upon regional changes in the thickness of the tracheid walls and the volume of the lumen, the one region merging into the other by somewhat gradual transitions and always without that sharply defined alteration of structure so characteristic of the growth rings in the Coniferales (plate 1). In existing *Araucarias* the "growth rings are not determinable, or at most poorly defined," though De Bary (13, 513) cites the case of a specimen of *A. excelsa* grown in the open ground, which showed sixteen sharply defined growth rings, and Kraus has

observed somewhat similar phenomena in the case of *A. brasiliensis*. Specimens coming under my own observation, but representing growth which was completed in a conservatory, show that in *A. excelsa* and *A. Cunninghamii* the growth rings are either not determinable or at most very imperfectly defined; while in *A. Bidwillii* they are only faintly defined by a slightly more open structure in the earliest spring wood. The same law holds true for fossil species in which it meets with only partial exceptions, as in *A. Edvardianum*. In *Dammara* the "growth rings are more or less clearly defined," approximating in this respect to what is found in the *Coniferales*, and between which and the typical *Cordaitales* they may be held to represent a transitional form.

Apart from those conditions of internal tension which arise incidentally to the formation of dissimilar tissues, and which induce structural alterations, growth rings may be regarded in the main as a direct expression of the alternation of sharply defined growth and rest periods; and since these in turn are correlated with sharply defined seasonal changes, such as are common to more northern latitudes, it becomes possible to utilize these facts in forming an approximate estimate of the general climatic conditions under which the tree must have developed. From this it is also possible to draw important inferences as to the climatic conditions which must have prevailed in earlier geological periods, as indicated by the presence or absence and the specific character of growth rings in fossil woods, a conclusion which gains force from the relation which the formation of growth rings in *Araucaria* bears to climatic conditions, as already stated.

Every growth ring presents two structurally dissimilar regions which correspond with different periods of activity, and it is the apposition of these in successive years which principally determines the recognition of the growth ring. The initial growth of a given year arises at the earliest possible moment at which the cambium is capable of generating new tissue. The elements which thus arise are applied directly to the outer face of the growth ring for the preceding year. In the formation of such

elements two important factors are involved. Owing to the peculiar conditions of growth attending their organization, they are formed under a minimum tension, in consequence of which they rapidly attain to relatively great size, and it is therefore found that the first tissue of the season is always most open. But this feature depends again upon the second factor. In consequence of the great excess of nutrition supplied during this period of growth, and the very rapid process of construction which follows, secondary growth of the walls is limited and these structures remain thin, while the lumens are correspondingly large. In transverse section such cells almost invariably show a greater length of the radial diameter, which is never less than the tangential. As growth advances there is a slight but progressive change whereby the secondary development of the wall increases somewhat and becomes constantly thicker; but the principal alteration occurs in the form of the cell in such manner that the radial and tangential diameters tend to equality. Such thin-walled structure is developed during the first four or six weeks of growth, and it is therefore designated as *spring wood*. Toward the end of the general growth period, which has elsewhere been shown to terminate by the second or third week of July for about ninety per cent of trees and shrubs in this latitude (80), the structural character of the ring is subject to more or less profound change as the rate of growth diminishes and the internal tension of the tissues increases. The isodiametric form of the tracheid is then replaced by an extension of the tangential diameter and a shortening of the radial diameter, the latter progressing more rapidly than the former. This alteration is of such a nature that in those tracheids which represent the last product of the season's growth the opposite tangential walls are closely approximated or even in actual contact, while the tangential dimension is sensibly increased as compared with tracheids of the same row in the spring wood. Coincident with these changes the secondary wall acquires an unusual prominence, and in many of the hard pines, as also in *Pseudotsuga*, it becomes so excessively thickened that the lumen is reduced to small dimensions

and not infrequently is almost obliterated. The *summer wood* thus characterized is also distinguished by its greater hardness, which in the Douglas fir imparts an almost flinty character to the structure; and commonly also, as exhibited in *Pseudotsuga Douglasii*, *Pinus palustris*, *P. resinosa*, etc., by a considerable amount of resinous matter, which, by reason of its definite color, establishes a more or less striking contrast between the two regions of growth. It is therefore obvious that the demarcation of the growth rings depends upon the direct apposition of spring and summer woods, each of which is characterized by special structural and other physical features.

The *transition* from the spring to the summer wood is *gradual* when there is no sharply defined limitation of the two zones, but the one seems to merge into the other by a series of more or less insensible gradations. This is exemplified in its typical form in the Cordaitales, and among the Coniferales it is a feature of the great majority of species. Under such circumstances the internal limits of the summer wood can be determined only approximately, and they are necessarily established where the greatest alteration of structure and color occur. Less frequently the transition is *abrupt*, as in the hard pines, notably *P. palustris*, or in the Douglas fir (plate 1). There is then a strong contrast between the two structural regions. A further variation of this relation is to be seen in those cases in which the somewhat gradual transition from the spring to the summer wood is followed the next year by a corresponding change to the spring wood. This is of rare occurrence and is to be met with in only one case, — *Pinus Torreyana*, — in which also such double graduation seems to arise only in the case of thick summer wood, since, when the latter is thin, the transition is *abrupt*. Rarely the summer wood exhibits a zonal development whereby it becomes doubled through the interposition of a zone of thin-walled and rather large-celled tissue. This finds its typical development in *Taxodium distichum*, of which it is a characteristic feature. It may also be met with occasionally among the higher Coniferales, especially among the hard pines. It is a constant feature of taxonomic value.

The relative volume of the spring and summer wood is subject to wide variation not only as between different genera and species but also as between individuals of the same species. While this depends in the first instance upon inherent qualities, it is also dependent to a very large extent upon conditions of growth. In *Juniperus* and some species of *Cupressus*, as also in *Torreya* and *Taxus*, the summer wood may constitute the bulk of the growth ring and render it impossible to determine where the spring wood ends. The opposite extreme is to be met with in the genus *Thuja* and in many species of *Cupressus*, where the summer wood is reduced to from two to six rows of tracheids, which are to be distinguished chiefly by their greater color and shorter radial diameters. The Douglas fir offers an excellent illustration of such variations within the limits of the species. This is shown by the following data, taken from five different trees, and also by plates 1 and 46.

RELATIVE VOLUMES OF SPRING AND SUMMER WOODS

	SEQUENCE VALUES	GROWTH RINGS IN MILLIMETERS			RATIOS
		Average Volume of Ring	Summer Wood Average Volume	Spring Wood Average Volume	
No. 2 . .	1	1.950	0.891	1.059	1:1.18
" 428 . .	2	2.725	1.110	1.615	1:1.45
" 789 . .	3	3.250	0.975	2.275	1:2.33
" 35 <sup>a</sup> . }	{	4.600	1.200	3.400	1:2.83
" 35 <sup>b</sup> . }		1.455	0.383	1.072	1:2.79
" . .	4	3.097	0.791	2.236	1:2.81
" 316 . .	5	5.100	0.950	4.150	1:4.37

While it is thus evident that estimates of relative volume are of no great value for purposes of exact differentiation, they nevertheless do serve a useful purpose in some instances, and they should always be taken into consideration in a diagnosis.

## CHAPTER III

### TRACHEIDS

In the Gymnosperms the woody structure of the stem is composed of more or less fibrous elements to which the generic term *tracheids* may be applied in conformity with the definition adopted by De Bary (13, 155), but which, for our present purposes, may be described as elements of indeterminate or more generally of determinate length, of either a prosenchymatous or parenchymatous type, and characterized chiefly by the presence of bordered pits. As such tracheids exhibit important variations among themselves, chiefly with respect to form, distribution, and structure, it is necessary to distinguish carefully between the various types entering into the structure of the woody axis. First of all it is possible to distinguish between those of the prosenchymatous type and those of the parenchymatous type, the differentiation being readily effected by means of the external form. Those of the parenchymatous type are to be met with in either the medullary rays, when they may be described as *ray tracheids*, or they arise in series parallel with the prosenchymatous elements with which they are therefore mingled as wood parenchyma, and they are to be distinguished as *parenchyma tracheids*. A further discussion of these forms will be deferred until they can be brought into connection with the general structures of which they form characteristic features, while at this time our attention may be directed more particularly to the tracheids of the prosenchymatous type. The fibrous tracheids are of two kinds, *spiral* and *pitted*. The *spiral tracheids* are chiefly met with in the protoxylem region of which they are characteristic and dominant elements and where they are of indeterminate length. Their spirals represent a secondary growth of the cell wall, and the latter is therefore devoid of pits

except in transitional forms. Rarely the spiral tracheids are met with in the secondary wood of which they then constitute the chief part. But in such situations the spirals represent a tertiary growth of the cell wall, which is also characterized by the presence of bordered pits in the secondary wall. Such tracheids are always of determinate length and their extremities are tapering.

The pitted tracheids are exclusively elements of the secondary wood of which they constitute the dominant features. They are of determinate length and their extremities are tapering. Their walls are characterized by the presence of peculiar pits which belong to the secondary layer, and they are devoid of spirals except in the case of *Taxus*, *Torreya*, *Pseudotsuga*, *Larix americana*, and *Pinus tæda*, where the spirals represent the tertiary layer of the wall. It follows that in this type the tracheids are characterized by the presence of both spirals and pits. Before proceeding to discuss these two forms of tracheids more in detail, a synoptical view of the tracheids as a whole may serve to make their relations more clear.

**TRACHEIDS.** Elements of a cylindrical or fibrous character, including vessels and their derivatives, together with certain specialized forms of a parenchymatous type, the whole distinguished by the presence of bordered pits upon their terminal, tangential, or chiefly upon their radial walls.

1. *Wood tracheids.* Elements which constitute the dominant structure of the so-called wood. They are as follows:
  - a. *Resinous.* Not structurally different from the pitted tracheids, but distinguished by the presence of resin, usually in the form of localized masses like transverse septa in the immediate vicinity of medullary rays. Common to the Cordaitales.
  - b. *Spiral.* Characterized by the presence of a spiral structure which is typical of the protoxylem of all genera and is of secondary origin; also of tertiary origin and typical of the secondary wood in special cases, being then accompanied by bordered pits.
  - c. *Pitted.* Characterized by the absence of spirals except in the special cases indicated in *b*, and by the uniform presence of bordered pits of secondary origin, chiefly on the radial walls; typical of the secondary wood in all genera.

2. *Wood parenchyma tracheids*. Usually short, cylindrical cells with thin walls, transverse terminal walls, and bordered pits. Confined to the higher Coniferæ.
  - a. *Parenchyma tracheids*. Characteristic of the xylem of the higher Coniferæ, with which their general direction of growth coincides. Found in association with the resin passages.
  - b. *Ray tracheids*. Characterized by their occurrence in the medullary rays with which their general direction of growth coincides.

We may now proceed to a more detailed consideration of the structure and distribution of the tracheids thus classified.

### SPIRAL TRACHEIDS

The spiral tracheids are so called because of certain narrow bands of secondary or tertiary growth which lie upon the inner face of the cell wall and take the form of definite spirals. These structures are found to present great diversity in the form of their transverse section, which, as shown many years since by De Bary (13, 156), may vary from elliptical or round-rectangular to an almost quadratic form. In general terms they may be described as ribbonlike and localized thickenings of the cell wall, which are designed for the obvious purpose of strengthening the latter. While this purpose is not always a prominent feature in the Coniferæ, it may nevertheless be recognized in the structure of the protoxylem, and it is conspicuously defined in those thin-walled elements to be met with among Pteridophytes or in the higher seed plants, notably in the spiral tracheids of *Zea*, in which there is a strong disproportion between the thickness of the initial wall and the volume of the cell. In more general terms, therefore, it may be looked for in succulent stems of vigorous growth rather than in those of a more woody character and slow growth; or it appears more frequently in plants of a primitive type of organization than in those of a more advanced type, in which the elements have experienced a more general growth in thickness, and where, in consequence, special contrivances for support are not demanded. From the standpoint of development, therefore, we may consider that the typical spiral



of the primitive forms has been lost through replacement by or through its being merged by extension and fusion into a growth which is continuous between all points of the cell wall. The capacity for the formation of spirals is thus eliminated from the greater portion of the structure of the wood, though survivals are commonly met with in many of the higher seed plants, where they impart to the wood more or less well defined characters of diagnostic value. This capacity is also lost most completely in the greater number of the Cordaitales, Ginkgoales, and Coniferales, — indeed, it may be said that for the secondary growth of the wall it is eventually lost in all species; but the tendency still survives, a fact made apparent by the observation that in certain species the tertiary layer of the wall invariably gives rise to such spirals, which then constitute definite and reliable diagnostic features, while in other species they are only imperfectly formed. In all such cases the spirals are to be regarded as survivals, — as the last phases of a tendency which elsewhere has become completely obliterated.

The origin of the spirals may be traced to a localized secondary growth of the cell wall. They constitute, in fact, the primitive form of the secondary wall which later becomes modified in accordance with altered conditions of growth in such way as to involve an obliteration of the spirals. Such changes are features of progressive development, in consequence of which it is generally true that such structures are always most prominent and abundant in the more primitive types, becoming more rare in plants of a higher type of organization and development. Similar relations exist as between the primary and secondary wood of all known Gymnosperms, whence it is possible to recognize the general law that spiral tracheids are a feature of the protoxylem, to which region they are wholly confined in the Coniferales and Ginkgoales, and almost strictly confined in the Cordaitales, being, with few exceptions among the higher Coniferales, wholly absent from the secondary xylem.

The direction of the spirals is constant in most cases, being right-handed or ascending from right to left on the side nearest

the observer. Usually more than one spiral is developed in the same tracheid, but it does not follow that the full number will be present at all points throughout the length of the tracheid. As between different genera and species, the number usually varies from one to four. This is much less than in the Angiosperms, where they may be as many as sixteen to twenty. Localization also occurs in such manner that the spirals often run in series, these latter being separated from one another by wider intervals, and as this relation is subject to somewhat wide variation within the same species, it follows that it cannot be utilized successfully for diagnostic purposes, although it is quite possible to recognize and define and utilize the more general differences of distribution in the terms *few* and *distant*, *numerous* and *approximate*. The variation in distribution above referred to is largely expressed in the fact that in the tracheids first formed in a season's growth the spirals will always be most widely separated, while those which are formed later constitute a more compact series. This fact becomes prominent wherever such structures can be observed through a considerable radial extent of wood, and it is therefore particularly well shown in growth rings, though it may also be seen in the protoxylem region when the latter is of great radial extent, as in *Cordia*. Thus in *Taxus* or *Torreya* or *Pseudotsuga* it may be seen that in passing from the earliest spring tracheids to the last-formed summer wood there is a graduated condensation of the spirals which agrees with the relative rate of development in the tracheids themselves. A similar variation is to be seen within the limits of an individual tracheid in such way that the spirals in the central region are more widely separated than those nearest the extremities. This has been adequately explained by De Bary (13, 157), who has shown the more distant coils to result from stretching of the walls during the period of very active development, but subsequently to the formation of the spirals; while the condensed forms would be an expression of a slower rate of growth in the cells or in special regions of them, in consequence of which the spirals more nearly retain their original relations to one another.

In the Coniferales the spirals throughout the entire extent of the protoxylem structure are more or less distinct, though there is a more or less definite tendency to coalescence. Such a tendency becomes most pronounced in the lower Gymnosperms, being especially well defined in the Cycadaceæ and the Cordaitaceæ. In the former the spirals become approximated and blend in such a manner as to definitely reduce the areas devoid of secondary growth, which then assume an elongated form; and as this latter diminishes still further in length, the spirals are eventually replaced by a more general thickening of the wall through secondary growth, and definite pits arise. Such changes are progressive from the protoxylem radially outward through the entire extent of the secondary wood, so that there is a definite series commencing internally with typically spiral elements and terminating outwardly with typically pitted elements, the two being connected by transitional forms. The same structural alterations may be seen in Cordaites, which offers a peculiarly instructive illustration of the process because of the regularity with which the changes arise and the extent of the structure in which they lie. As these transformations which are completed within the transition zone are of great phylogenetic importance as well as of taxonomic interest, it will be necessary to trace them somewhat in detail as they appear in Cordaites Brandlingii.

In the protoxylem region the structure is wholly composed of spiral tracheids (plate 3). In the successive radial development of new tracheids there is a constant tendency to a more uniform thickening of the cell wall by a secondary growth. This at first finds expression in the more compact arrangement of the spirals (plate 4), which later coalesce at various points, thus giving rise to more localized areas devoid of secondary thickening, and hence to a scalariform structure in which the general lines conform more or less closely to the direction of the original spirals (plate 5). By a further modification the elongated, thin areas become converted into shorter, often isodiametric areas substantially by a process of division. A further tendency to general thickening of the walls causes the margins of the scalariform

structure to project from all sides and extend over the area of arrested growth as a lip which never completely closes at the center, where there is left a usually circular, sometimes oval or again lenticular or even oblong, opening, and in this manner the bordered pit is formed (plate 6).

From the statements so far presented it may be correctly inferred that the structural alterations which arise within the transition zone are subject to great variations, whereby the change from spirals to bordered pits may arise very gradually through a broad, radial zone, as in *Cordaia Brandlingii*, or it may take place very abruptly, as in the modern *Coniferæ*. The general tendency of such evidence is to show that with a higher type of organization there is a corresponding diminution in the transition zone and an increased abruptness in the structural alterations. The logical result of an extension of this process would be the reduction of the bordered pit to the condition of a simple pit, and ultimately to its complete obliteration. In the *Coniferæ* the reduction of the bordered pit to a simple pit sometimes occurs in the case of medullary rays or even in the case of tracheids with very thick walls, but it becomes most prominent in the *Angiosperms*, where it is a characteristic feature. Instances also occur in some of the hard pines, in which the pit is completely obliterated. This applies in particular to tracheids of the summer wood, the walls of which have become unusually thickened.

The relations to which attention has thus been directed somewhat in detail have been expressed in more general terms by De Bary (13, 321) in the statement that, "Outside the primitive elements wider tracheæ follow. Their development takes place successively, advancing from the inner edge of the bundle outwards, and, as a rule, at a time when the elongation of the entire part to which they belong is nearly at an end. The thickenings on their walls, therefore, have a successively denser arrangement; dense spirals and annular tracheæ, then reticulated and pitted tracheæ, follow one another in succession from within outwards, with gradual transitions, or with the omission of

one or the other intermediate form." It is probably a justifiable inference from the preceding facts that the relation which exists between the spiral tracheids of the protoxylem and the pitted tracheids of the secondary xylem in the Coniferæ is, in general terms and from the standpoint of development, the same as that exhibited between the lower and higher types of vascular plants.

Inasmuch as specimens derived from fossil woods or from recent woods which have been employed for constructive purposes will almost invariably represent some portion of the secondary wood only, it follows that in all but exceptional cases the spiral structures so far considered will be entirely absent, and in those few instances in which they may occur the determination that they belong to the protoxylem region can be made without difficulty. It is nevertheless true that in a few genera definite spirals are to be met with in the secondary wood structure of which they may then be characteristic features throughout the entire extent of the growth rings, or they may be more or less localized. Such spirals, which are obviously of an exceptional nature, are features in the development of the tertiary wall of the tracheid, and they are therefore characteristics of thick-walled elements. In all their essential characteristics of form and distribution they conform to the laws which govern the spirals of the secondary wall, but they show a marked tendency to obliteration through degeneration in the relatively thicker walls. Thus in the genus *Taxus* or *Torreya* such spirals are common to all the tracheids of the growth ring, but in *Larix*, as also in *Pinus tæda*, in both of which the walls are relatively thicker, the spirals are reduced to a vestigial form, being sporadic and in the one case distant, while in the other case the individual spirals are only partially developed. This law is more exactly and specifically illustrated in *Pseudotsuga*, where there is a strong contrast between the thin-walled spring wood and the very thick-walled summer wood. In the former the spirals are perfectly formed and constant, and they bear a very strong resemblance to what may be observed in the *Taxaceæ*. In the

latter case, however, the spirals are either sporadic and vestigial (*P. Douglasii*) or they are often almost completely obliterated (*P. macrocarpa*). So well defined and constant are these relations that they serve as an important differential character for the genus.

Tracheids with spirals developed in the tertiary layer of the wall are thus seen to be typical features of *Taxus*, *Torreya*, and *Pseudotsuga*, while they are also more or less distinctive features of *Larix americana* and *Pinus tæda*.

In all investigated species of *Torreya* there is a rather wide variation in the angle which the spirals make with the axis of growth, and this becomes most pronounced in *T. californica*, which gives the lowest angle for any species of either *Torreya* or *Taxus*. Usually the spiral has an angle quite distinct from that of the lines of striation in the cell wall, but in *Torreya taxifolia* (fig. 1) the two often coincide.

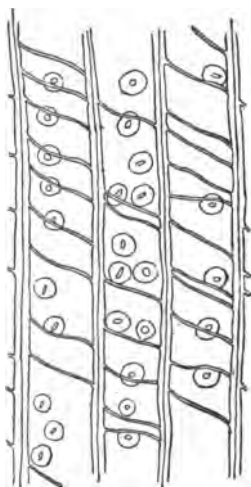


FIG. 1. *TORREYA TAXIFOLIA*.  
Radial section showing  
spirals of tracheids and  
bordered pits.  $\times 210$

The following will show the various details derived from the average of ten measurements for each species:

	AVERAGE ANGLE	HIGHEST ANGLE	LOWEST ANGLE	EXTREME RANGE
<i>Torreya nucifera</i> . .	70.5°	87.0°	57.0°	30.0°
<i>Torreya taxifolia</i> . .	70.4	77.0	61.0	16.0
<i>Torreya californica</i> .	46.2	63.0	30.0	33.0
Means . . . . .	62.3°	75.7°	49.3°	26.3°

In the genus *Taxus* (fig. 2) the spirals are rather close and in two, rarely three, series. As in *Torreya*, they are typical throughout the spring wood, but with a pronounced tendency to obliteration in the summer wood. This tendency is subject to considerable

variation in different species. In *T. canadensis* the spirals are conspicuous throughout. In *T. floridana* they usually disappear in

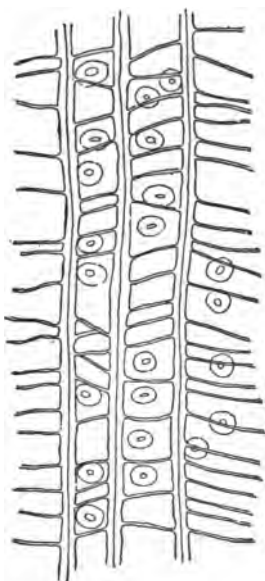


FIG. 2. *TAXUS BREVIFOLIA*.  
Radial section showing  
spirals of tracheids and  
bordered pits.  $\times 210$

the later growth, and are wholly wanting in the two or three last-formed tracheids. In *T. brevifolia* they become very imperfect in the outer summer wood and tend to disappear completely, only vestiges remaining in the last-formed tracheids. In *T. cuspidata* the spirals are generally absent from the summer wood, or when present are merely vestigial. The angle is somewhat greater—about 7 degrees—than in *Torreya*, and with respect to certain species this fact is apparent without special measurement. The four species appear to be paired off in such a way as to represent a mean difference of about 10.9 degrees as between *T. canadensis* and *T. floridana* on the one hand, and *T. brevifolia* and *T. cuspidata* on the other. In all cases the angles of the spirals are quite distinct from those of the lines of striation. The follow-

ing details are based upon an average of ten determinations:

	AVERAGE ANGLE	HIGHEST ANGLE	LOWEST ANGLE	EXTREME RANGE	MEAN OF TWO
<i>Taxus canadensis</i> . . .	72.4°	88.0°	66.0°	22.0°	75.4
<i>Taxus floridana</i> . . .	78.4	90.0	72.0	18.0	
<i>Taxus brevifolia</i> . . .	63.0	76.0	55.0	21.0	64.5
<i>Taxus cuspidata</i> . . .	66.1	87.0	45.0	42.0	
Means . . . . .	69.9°	85.2°	59.5°	25.7°	

A comparison of these results in detail emphasizes the fact that the distribution of the spirals, as between spring and summer wood, is in direct harmony with the principles already

stated, and furthermore that the angles at which the spirals develop do not afford an adequate basis for generic differentiation. It is nevertheless possible to recognize subgeneric groups in such wise that in both genera a general line of division may be established at 70 degrees. In the case of *Torreya californica* the very low angle of 46.2 degrees may be regarded as a differential character of specific value.

In the genus *Pseudotsuga* spirals are confined to the tracheids of the spring wood. This has a partial exception in *P. macrocarpa*, in which vestigial spirals may be observed in the tracheids of the earlier summer wood. In this species the mean angle is 70 degrees, but the spirals are always characterized by lack of prominence, they are often widely distant, and the somewhat extended areas within which they are wholly wanting or fragmentary suggests a process of obliteration. In *P. Douglasii* the average angle is 82 degrees; the spirals are characterized by considerable prominence and they are also, on the whole, close. In *P. miocena* the angle ranges from 49 degrees to 83 degrees, with a probable mean of about 65 degrees, from which it would seem likely that this species occupies a position superior to that of *P. macrocarpa*, but this relation cannot be determined with certainty on account of the difficulty of ascertaining their distribution within the limits of the summer wood. In the genus as a whole the angle, the prominence of the spirals, and the closeness of the turns obviously possess well-defined differential value with respect to the limitations of the species.

Among the higher genera of the Coniferæ only two cases are known in which spirals occur, but in each the character is of a very sporadic nature. In *Larix americana* the spirals are frequently found in the summer wood, but they are so inconstant in their occurrence and present such varying aspects that the angle cannot be determined. In *Pinus tæda*, where the walls of the summer tracheids are very thick, rudiments of spirals may sometimes be seen. Here also it is manifestly impossible to determine the angle.



Viewing these five genera collectively, their spirals conform fully, in their occurrence and relation to progressive development, to the general principles already stated, and especially as formulated by De Bary. They possess no differential value of generic rank with respect to *Pinus* and *Larix*, but they do have such value with respect to *Torreya* and *Taxus* on the one hand and *Pseudotsuga* on the other, the differentiation resting upon their occurrence in the summer wood in the former and their exclusion from that region in the latter. Were any question to arise in this connection, it could be authoritatively decided by the definite association of resin passages and fusiform rays in *Pseudotsuga*.

It only remains to determine how far such structural features may be employed as a basis upon which to determine the general phylogeny of the genera. Between *Torreya* and *Taxus* there is very little upon which to base conclusions respecting sequence in development, and it is apparent that both of these genera have attained to nearly the same level. Such differences as do exist, however, seem to point to the relatively though slightly inferior position of *Torreya* as indicated by (1) the smaller angle in that genus, and (2) the generally more compact spirals of *Taxus*. This view, so far as it possesses phylogenetic value, appears to confirm the conclusions respecting the relative positions of these two genera as already determined upon the basis of external morphology and stated by Eichler (15, 103).

It is fairly clear, from the facts at hand, that all such spirals as are to be met with in the higher Coniferales are to be regarded as survivals of structures which gained greater prominence in a more primitive state of development of the organism. They do not, therefore, indicate simple parallelisms between plants occupying a similar horizon in the scale of development, but they rather direct attention to derivation from a common ancestry, and, as previously pointed out (59, 255), they lead us to the consideration that *Torreya*, *Taxus*, *Pseudotsuga*, *Larix*, and *Pinus* represent different branches of a general phylum, — undoubtedly also including other closely related genera in which the spirals

have been wholly obliterated, — which had its origin at a point anterior even to such types as Cordaites, and therefore in a group probably represented by the Cycadofilices.

## PITTED TRACHEIDS

The *pitted tracheids* may be so distinguished because of the invariable presence of bordered pits upon their radial and, under some circumstances also, upon their tangential walls. Such pits belong to the secondary layer of the cell wall in all cases. In comparatively few instances such pits may be associated with spirals in the tertiary wall, when the two structures will be found so related that while the latter may overlap the former, the orifice always lies between the turns of the spirals (figs. 1 and 2).

In their transverse aspect there is no feature which may be employed to distinguish the pitted from the spiral tracheids. In the longitudinal aspect the former differs from the more primitive forms of the spiral tracheid with respect to length and definite terminations in such way that the one is a wood cell while the other is a vessel, but between the two no sharp line of demarcation can be drawn, since, as already indicated, they pass the one into the other by insensible gradations.

All tracheids exhibit the same structural features with respect to the development and composition of the wall, and as a knowledge of these is antecedent to a correct understanding of certain alterations which arise incidentally to growth and also to decay, it will be desirable to examine into the structure of the wall somewhat in detail.

Assuming the primitive form of the cell to be that of a sphere, this form undergoes alteration in accordance with the immediate environment whereby growth first of all becomes excessive in one direction coincident with the axis of growth for the plant as a whole, while it remains practically equal in the radial and tangential planes which cut the first at right angles. From this it follows that while in a longitudinal aspect the tracheid is always presented as a fibrous element with tapering extremities,

in a transverse section it approximates more nearly to the primitive form and thereby exhibits a hexagonal outline as directly derived from the circular by mutual compression of contiguous elements. As the woody elements arise by division, their tendency at first is to assume the spherical form; hence they split away from one another. But such separation is never fully completed; in fact, it is never developed to any marked extent in woody tissues and it remains localized. The separation is usually confined to the angles of the tracheids, and it results in the

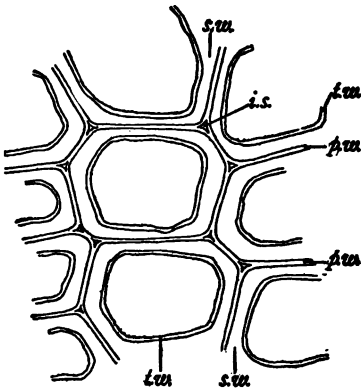


FIG. 3. *PSEUDOTSUGA DOUGLASII*.  
Transverse section showing the structure of the cell wall: *p.w.*, primary wall; *s.w.*, secondary wall; *t.w.*, tertiary wall; *i.s.*, intercellular space.  
× 350

formation of *intercellular spaces*, which therefore originate *schizogenously* (fig. 3). In the subsequent modification of the wall by secondary growth these spaces, when not too large, are commonly obliterated by infiltration. The presence of such intercellular spaces always emphasizes the fact that what appears as a single membrane is in reality a double wall, one half of which belongs to each of the adjacent cavities.

In the secondary growth of the wall new layers are laid down on opposite sides of this *primary wall* (fig. 3), and in their develop-

ment they give the dominant features of thickness, color, and hardness (fig. 3, *s.w.*). When brought into such relations the primary wall, apparently lying between two cells, is often designated the *intercellular substance*. The secondary wall not only exhibits very variable development in thickness according to the conditions of growth, as between the spring and the summer woods, but its growth is also more or less localized, and there thus arise such structural features as have already been described in the spiral tracheids, or such as will be discussed more in detail in a subsequent chapter under the title of "Bordered Pits." Upon

the inner face of the secondary wall there is what is known as the *tertiary wall* (fig. 3, *t.w.*). This is of limited volume in the great majority of cases, and it is to be recognized as a thin layer. It rarely attains any prominence or contributes to the structural variation of the tracheid, but in *Taxus*, *Torreya*, and *Pseudotsuga* it does follow the same course of development as the secondary wall of the primitive tracheids, and develops spirals which are constant and distinctive structural features. Vestiges of such tertiary spirals are to be found also in *Larix* and *Pinus*, and wherever they occur they are to be interpreted as representing a phase in the degeneration of the spiral structure which has already permanently disappeared from the secondary wall but survives in the tertiary wall to a certain extent. In any transverse section of a thick-walled tracheid, under favorable conditions, we may observe fine lines disposed concentrically with one another and with the primary wall. These represent the *stratification* of the secondary wall, and they are substantially due to the process of upbuilding by successive layers. In a longitudinal aspect the wall also shows a series of fine lines cutting the axis of the tracheid and the lines of stratification diagonally, or in a transverse section cutting the latter radially. These represent the lines of *striation*, due probably to localization of water of organization along definite planes of growth. They are not readily observable under ordinary conditions, but when the cells are macerated in potassium hydrate they stand out with great prominence, and it will be seen in a subsequent chapter that the same effect is also produced by decay.

The substance of the cell wall consists primarily of cellulose, represented by the formula  $C_6H_{10}O_5$ , but in the course of growth alterations arise through the introduction of carbohydrate bodies of various kinds, so that the composition can no longer be represented by such a simple formula. Thus in the primary cell wall there is usually a large amount of *pectin*, which may be differentiated and localized by ruthenium red, which develops a bright cherry or rose-red color and affords a very delicate test. In the secondary walls also the cellulose represents

various modifications which may all be embraced under the comprehensive term *lignin*. Such *lignification* is, in general terms, characteristic of the woody tissue of all plants in various degrees, but usually in such manner that the hardness of the parts is directly related to the extent of lignification. The differences thus briefly indicated not only bear an important relation to the action of various chemical reagents and stains, but they are of the first importance in explaining the variable phenomena of decay; since it is found that neither chemical agents, stains, nor decay act uniformly upon all parts of the cell wall, their action varying according to locality as well as according to the particular agent or the specific organism concerned. It will therefore be profitable to inquire somewhat more closely into these relations.

According to Weiss (75, 61) the percentage composition of the unaltered cellulose may be taken as  $C_{44.4}H_{6.18}O_{49.88}$ . In the course of growth, however, alterations of various kinds arise through the introduction of carbohydrate bodies of various kinds, though all belonging to the cellulose group, so that the composition can no longer be represented by such a simple formula as that given. The composition of these secondary products or incrusting substances, though somewhat widely different in different plants, may be said to vary within an approximate percentage range of 5.99 for carbon, 0.53 for hydrogen, and 8.15 for oxygen, while their mean composition may be stated as C 50.7, H 6.08, O 43.03 per cent. On the other hand, the incrustation substance from the same plant (*Fagus sylvatica*) may be found to vary from C 48.10, H 6.09, O 47.81 per cent to C 67.91, H 6.89, O 25.20 per cent. A comparison of these modified forms with normal cellulose brings out the important fact that while there is essentially no change in the percentage proportion of hydrogen, the oxygen has been reduced in varying quantities from 1.57 per cent to 24.18 per cent with a corresponding increase in the relative proportion of carbon.

Accompanying changes of the nature thus far discussed — the formation of the secondary wall and the deposition of lignin substance — are always associated with the deposition of mineral

matter which is localized in the cell walls as the only way provided for the disposal of waste matter. Such mineral salts are important factors in imparting an increased specific gravity and a greater element of hardness to the structure as a whole, while they appear upon combustion in the form of an unoxidizable ash residue, which varies in the North American Coniferæ from 0.08 per cent in *Libocedrus* and *Pseudotsuga* — in specific cases of the latter falling as low as 0.02 per cent — to 1.34 per cent in *Torreya taxifolia* (65, 333).

The variations in the cell wall thus noted are accompanied and more or less exactly indicated by the reactions of the wall toward chemical reagents and stains. Thus aniline chloride or sulphate imparts a brilliant yellow color to the entire lignified membrane, serving at the same time to differentiate the primary from the secondary walls by virtue of the greater depth of color and the greater degree of translucency imparted to the former. Iodine is absorbed with great energy by all parts, but rather more strongly by the primary wall, which thereby acquires a deeper yellow or yellowish brown. When lignified membranes are treated with strong sulphuric acid the secondary wall is attacked and brought into solution, while the primary wall is left intact if the action be properly limited. In this case the action is one of hydrolysis. On the contrary, a strong oxidizing agent, such as Schulze's maceration, acts first upon the primary wall, thereby separating the secondary walls from one another; or, in accordance with Mangin's reaction with alcohol and hydrochloric acid, whereby the pectic acid is set free from its original combinations, it is possible not only to secure a more intense reaction with ruthenium red but also to separate the cells from one another when the pectic acid has been neutralized by ammonia. Similar disintegrations may be effected in the primary wall by other reagents, in which case they constitute the scientific basis for such important economic processes as are involved in the manufacture of wood pulp by chemical means.

The total thickness attained by the cell wall necessarily varies as between the spring wood and the summer wood. This relation

is subject to somewhat wide variation as between different species and genera, and it is also found to be of a marked nature, even in the same species under different conditions of growth. For more extended details reference should be made to the table in Appendix A, but for our present purposes a few examples may be selected. Thus in all three of the investigated species of *Araucaria* the ratio of the walls — spring to summer wood — is 1 : 1, a relation which exactly corresponds with the absence of growth rings. In *Juniperus virginiana* the ratio is 1 : 2; in *Cryptomeria japonica* it is 1 : 4; in *Tsuga Sieboldii* it is 1 : 5. On the other hand, the same species may exhibit two ratios as determined by the peculiar conditions of environment under which the growth has been formed. Thus in *Taxus canadensis* we may have  $\left. \begin{smallmatrix} 2.4 \\ 4.8 \end{smallmatrix} \right\} : 4.8 \mu$ ; in *Larix Lyallii*  $\left. \begin{smallmatrix} 4.8 \\ 1.8 \end{smallmatrix} \right\} : 8.4 \mu$ ; and in *Libocedrus decurrens* we may get  $1.4 : \left\{ \begin{smallmatrix} 2.4 \\ 4.8 \end{smallmatrix} \right. \mu$ . While, therefore, it is obvious that there are certain ratio differences between the walls of these two structural regions, — differences which are more or less directly associated with species, — and while such differences may be of some value in confirming conclusions derived from other data, they are not of such a nature as to permit the formulation of a general law applicable to species in such a way as to establish a precise differentiation, since variation arises within the same species as a result of different internal and external conditions of growth, such as tension, soil, and climate, the latter being influenced by situation and exposure. In many cases, where the actual thickness of the walls is the same, the apparent thickness will vary considerably. This is directly attributable to differences in the transverse volume of the tracheid, whereby the spring tracheid, from its greater size, will have a wall relatively thinner, and thus apparently thinner than that of the summer wood. Our investigations show that for twenty genera and one hundred and fourteen species the mean ratio is 1 : 2.12. The following summary for genera may be consulted in this connection :

TABLE OF RATIOS FOR THE TRACHEID WALLS—GENERA

	VOLUME OF TRACHEID, SUMMER TO SPRING WOOD IN TRANSVERSE SECTION	THICKNESS OF WALLS, SPRING TO SUMMER WOOD	NUMBER OF SPECIES FOR AVERAGE
Dammara . . .	1:1.80	1:1.66	1
Araucaria . . .	1:1.10	1:1.00	3
Ginkgo . . . .	1:3.64	1:1.33	1
Torreya . . . .	1:1.62	1:1.99	3
Taxus . . . . .	1:1.67	1:1.56	4
Thujaopsis . . .	1:1.13	1:2.50	1
Cryptomeria . .	1:1.68	1:4.00	1
Podocarpus . . .	1:2.01	1:1.43	1
Taxodium . . . .	1:1.25	1:2.00	1
Libocedrus . . .	1:2.60	{ 1:1.70 1:3.43 }	1
Thuja . . . . .	1:2.26	1:2.88	3
Sequoia . . . . .	1:2.51	1:2.75	2
Cupressus . . . .	1:1.98	1:1.71	9
Juniperus . . . .	1:2.24	1:1.43	11
Abies . . . . .	1:2.35	1:2.27	11
Tsuga . . . . .	1:1.97	1:3.01	5
Pseudotsuga . . .	1:2.31	1:2.95	2
Larix . . . . .	1:2.76	1:2.86	4
Picea . . . . .	1:2.12	1:2.27	9
Pinus . . . . .	1:1.98	1:1.97	41
Grand average . .	1:1.95	1:2.12	114

Variations in the transverse volume of the tracheid as expressed in square microns constitute the most prominent feature of any transverse section. They are expressed most conspicuously between the spring and summer woods, and they are due to the same causes which operate in the formation of the ring itself. Their relations are such that the earliest spring tracheids are always of greatest volume, but there is a progressive diminution radially outward at a somewhat uniform rate. At a certain point in radial development, however, there will usually be found a somewhat more marked alteration, which in specific cases becomes most pronounced—*Pinus palustris*—and results in an abrupt transition from one zone to the other. In other cases—*Taxus*



and *Torreya* (plates 20 and 22) — the transition is so gradual that it is often difficult or impossible to establish the exact boundary between the spring and summer woods. Such diminution in volume is accompanied by alteration of the two axes in such a manner that the tangential is steadily lengthened while the radial is correspondingly shortened. It is, therefore, commonly found that in the last-formed cells of the season the tangential diameter is somewhat longer in accommodation to the increased circumference of the zone, while the radial diameter is so shortened that the opposite walls are closely approximated or even in direct contact.

The relative volume of the spring and summer tracheids is subject to somewhat wide variation within the limits of the genera, being in the ratio of 1 : 1.10 for *Araucaria*, where there is practically no distinction of the two zones, and of 1 : 3.64 in *Gingko*, where there is a correspondingly sharp definition. The mean ratio for twenty genera, represented by 114 species, is 1 : 1.95. Within species limits similar variations arise, the most marked extremes being represented by *Sequoia* and *Juniperus*. In the former case the ratio varies from 1 : 1.77 in *S. gigantea* to 1 : 3.26 in *S. sempervirens*. In the latter genus the variation lies between 1 : 1.33 in *J. conjugens* and 1 : 4.4 in *J. sabina*. A somewhat extended study of the Douglas fir has given an opportunity to examine these differences with respect to a somewhat wide range of individuals. Thus in seven specimens taken without special selection, the following values are found :

No. 1.	1 : 1.91	} Regional variations in the same specimen.
2.	1 : 2.83	
3.	1 : 1.14	
4.	1 : 3.23	
5.	1 : 2.10	} Regional variations in the same specimen.
6.	1 : 1.92	
7.	1 : 2.14	
8.	1 : 2.50	
9.	1 : 1.70	} Regional variations in the same specimen.
10.	1 : 2.68	

The mean ratio for all these specimens is 1 : 2.21, which very closely approximates to that for *P. macrocarpa* (1 : 2.41), and it shows that the spring tracheid is normally twice the volume of the summer tracheid. But such a ratio is subject to important exceptions within the limits of the individual. Thus the values for 1 and 2 relate to regional differences in the same specimen, and the same is also true of 5 and 6, and 9 and 10. It is therefore obvious that such variations are in no sense of specific value for diagnostic purposes, since they are often as widely divergent within the limits of the species as between different species, being determined by peculiar conditions of growth. Inasmuch as variations in the relative volume of the tracheids is a feature of the density of the wood as a whole, it may be supposed to bear a certain relation to the strength of material and so to the value of the wood for constructive purposes, but this has been shown not to be the case (52, 39).

#### RESINOUS TRACHEIDS

In *Araucaria excelsa* a transverse section shows more or less numerous elements containing resin. These are not to be distinguished in their general structure from the surrounding tracheids, and they are to be recognized solely by their contents, which are usually somewhat prominent. Their distribution is characteristic. They occur in small, scattered groups, or more commonly in rows one or two elements wide, parallel with the medullary rays and in immediate contact with them on each side. When the plane of section passes near the position of apparently terminal walls, the latter are cut through in various ways, but they never exhibit any structural features, and they are therefore in no way comparable with the terminal walls of the wood-parenchyma cells. In a radial section these elements are seen to be long and fusiform, exactly resembling the wood tracheids except for reddish-brown, transverse plates which occur either close to or exactly opposite a medullary ray, — a position which is more clearly seen in a tangential section (fig. 4).

The dark plates closely resemble Sanio's bands, for which they might very readily be mistaken upon casual observation, or they

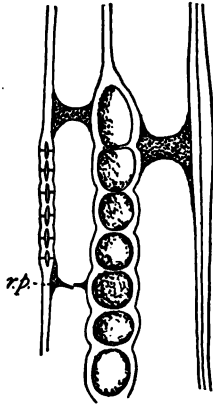


FIG. 4. *DAMMARA AUSTRALIS*. Tangential section showing the relation of the resin plates and the medullary ray, and a fractured plate (*r.p.*).  $\times 225$

might likewise be mistaken for terminal and unpitted walls. In *Dammara australis* these features are presented in their typical form. The transverse section shows such elements to be numerous and disposed in radial rows on each side of the medullary ray (fig. 5). In a radial section they present the same fibrous and fusiform character as in *Araucaria*, but, in addition, the wall usually experiences a marked increase in secondary growth within the region

exactly opposite a ray (fig. 6). This feature is also prominent in the transverse section (fig. 5). Such local increase in thickness always arises in adjacent cells in such a way that the more strongly thickened regions are exactly opposite, and they serve to constrict the cell cavity gradually from above and below, in such manner as to leave a channel about half the usual width of the cell cavity, which gradually widens upward and downward (fig. 6). It is at the position of maximum constriction that we find a transverse plate of variable thickness, but always of a reddish-brown color. These plates are always thinnest in their central region, and they may be of uniform thickness for the greater part of their extent.

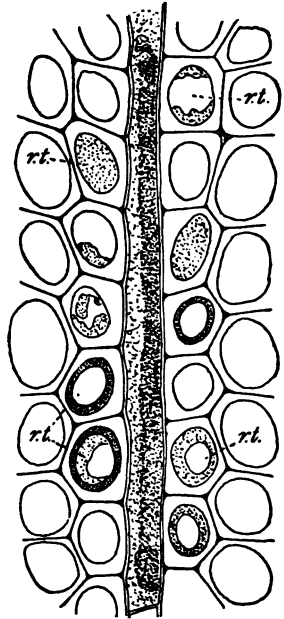


FIG. 5. *DAMMARA AUSTRALIS*. Transverse section showing the disposition of the resinous tracheids on opposite sides of the medullary ray at *r.t.*  $\times 300$

At the region of contact with the tracheid wall they become thicker and thereby attain a vertical distribution to an extent four or five times greater than the general thickness. At such position also there is a somewhat clear differentiation between the plate and the wall of cellulose in point of color. Such plates show absolutely nothing of the nature of pits, and they are in no sense comparable with the terminal walls of the wood-parenchyma cells, except in form and position (fig. 6). The peculiar position of these plates, their resinous color, and their simulation of both Sanio's bands and terminal walls excited a suspicion as to their true nature, and led to the belief that they might not be structural features at all. They were therefore subjected to a series of careful tests to determine (1) if they were structural, (2) if they were resinous, and (3), if the latter, to what extent. It was recalled in this connection that, although devoid of any special secretory reservoirs in the wood, *Dammara* is nevertheless well known for its production of the resin known as kauri or gum dammar. It was suspected that the plates might be local deposits of resin, and they

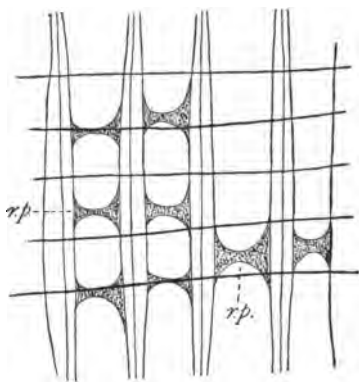


FIG. 6. *DAMMARA AUSTRALIS*. Radial section showing the local thickening of the tracheid wall, and the occurrence of resin plates (*r.p.*) opposite a medullary ray.  $\times 225$

were therefore brought into direct comparison with gum dammar, the characteristics of which are well known and described by Wittstein (77, 63). Tests were applied to thin radial and tangential sections, employing for this purpose (1) various essential and fixed oils, (2) ether, (3) alcohol, (4) ammonia, (5) potassium hydrate in  $1\frac{1}{2}$  per cent solution, and (6) concentrated cupric acetate. The plates were found to be very refractory with respect to all these reagents, and in all cases no change was to be observed, even after the action had extended over a period of several weeks, except partially in the case of ether and

alcohol, and completely in the case of potassium hydrate. In the ether reaction there did appear to be a certain diminution in volume, apparently through solution, when the reagent was first applied, but after that there was no further alteration. The application of alcohol, both in the hot and in the cold, showed that while the resin contained in the medullary rays was all dissolved, the plates were only partially affected. The reaction of the reagent was chiefly manifested in the development of strong curvature, often accompanied by fracture (fig. 4, *r.p.*). This was evidently due to an increase in volume as the first tendency toward solution, and it gave the first definite evidence that the plates could not be of a cellulose character. Beyond this

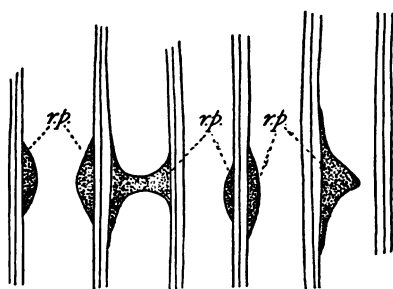


FIG. 7. *DAMMARA AUSTRALIS*. Radial section showing the origin of the resin plates (*r.p.*).  $\times 225$

no further change was brought about, even after several weeks of action. The potassium hydrate gave the most positive results. At first there was no apparent change, but after an interval of about ten days or two weeks the plates were found to have completely disappeared, leaving a perfectly clear channel in the cell cavity.

A further proof of the resinous character of these plates is to be found in the ruptures which they not infrequently exhibit (fig. 4, *r.p.*), and in the various developmental stages which may be observed without difficulty (fig. 7). These show that the resin gathers locally upon the inner face of the tracheid wall, and as its volume increases it projects from all sides toward the center, where it coalesces to form a continuous and imperforate septum. The facts thus obtained prove most conclusively that the plates are not cellulose, and although immersion in concentrated cupric acetate for eight weeks failed to develop the characteristic reaction, they point to the idea that the plates are probably resinous. The conclusion is probably justifiable that they consist of gum dammar,

which they closely resemble in many of their reactions, but of a highly refractory and modified character. The same evidence also conclusively shows that the cells in which the plates are developed are normal wood tracheids and not wood parenchyma, which is altogether unknown in any of the Cordaitales. Any transverse section of the wood of Cordaites will show these resinous plates to be present, usually in much larger numbers than in either *Dammara* or *Araucaria*, and they exhibit the same features in distribution (plate 12). Compare also plates 14 and 16.

We are naturally led to ask, What is the purpose of these resin plates? The peculiar form in which the resin is deposited and the particular location of the plates points with much force to their connection with some functional activity, since if it were simply a question of the storage of secreted products, the latter would hardly be disposed as found, but rather after the manner common to so many of the Cupressineæ; and this suggestion gains strength from the fact that with respect to the peculiar form of the resin masses as well as their location in the tissue, the Cordaitales are peculiar among the Gymnosperms. No exact comparison can be established with other plants, and it is difficult to suggest an adequate explanation. One thing does seem clear, however, and that is that since these plates are of an impervious nature and developed in some cases, at least, in connection with a special constriction of the tracheid cavity, they offer and possibly are specially designed to afford a definite obstruction to circulation in a vertical direction. In this sense they may be designed to serve the same general purpose that is accomplished by the development of thyloses in the vessels of the Angiosperms or in the resin passages of the higher Coniferales. It is therefore possible that they may be connected in some way, not at present clear, with a more complete restriction of the circulation to a horizontal direction, and particularly through the medium of the medullary rays as specialized channels for that purpose. Among existing Gymnosperms resinous tracheids are almost exclusively confined to *Dammara* and *Araucaria*, though it is a noteworthy fact that similar structures occur rarely

among the higher Coniferales. In the genus *Abies* they are prominent features in both *A. Fraseri* and *A. grandis*. In the former a transverse section shows them to be prominent and scattering through the summer wood, more rarely in the spring wood; while in the radial section the resin is seen to be massive in the summer wood, forming a peripheral layer in the spring wood. In *A. grandis* the resin is usually more abundant, but otherwise the features are the same.

The taxonomic value of the resinous tracheids applies exclusively to the Cordaitales, where they are of ordinal value, though in *Dammara* and *Araucaria* they may also become of specific value. In *Abies* they are so sporadic and present so little constancy as to be of no value.

From a phylogenetic point of view it is possible to determine the position which they occupy in the general scale of development, and so to utilize them in determining the position of plants in which they may occur. That they are met with in their most characteristic form almost exclusively in one of the most ancient, as also in one of the relatively primitive, groups of Gymnosperms points with force to the idea of their being also a primitive form of the secretory reservoir. This view is greatly strengthened by the fact that in such plants there are no special secretory reservoirs such as may be met with in the higher Coniferae, nor do we even find specialized wood-parenchyma cells devoted to such purpose. In this sense the sequence of the resin-producing structures would be (1) resinous tracheids, (2) resin cells, (3) resin cysts, (4) resin passages. The relation of such a sequence to the general phylogeny would be that, since resinous tracheids appear in a sporadic form in *Abies* and thereby represent a limited survival of a primitive character, the Coniferales have a common origin with the Cordaitales, which, developing as a lateral member of the main phylum, has retained this feature as an essential characteristic while it has disappeared almost completely from the main line of descent. Such obliteration is fully expressed in the Ginkgoales, which have also been developed as an offshoot from the parent stem.

## CHAPTER IV

### BORDERED PITS

In a preceding chapter it has been shown how the bordered pit originates in the spiral structure of the protoxylem through a more general and continuous development of the secondary layer of the cell wall. We are now concerned with an inquiry into the detailed structure of these markings, their variations under different conditions of growth and situation, and their relations to taxonomy as well as to phylogeny.

It has been seen that in the genesis of the bordered pit the bands of adjacent spirals or the bars of a scalariform structure generally enlarge toward one another so that the intervening area contracts about a common center, but the edges never completely meet, so that a pit is left at the central point. In such contraction, however, the secondary wall is not joined to the primary, but is free and springs from it as an arch which has a circular outline and a central orifice (fig. 8). As such pits are always paired on opposite sides of the primary wall, the entire structure, when seen in tangential section, is lenticular in form (fig. 11), with a membrane traversing the central plane and two openings opposite to one another at the extremities of the minor axis. From this it is obvious that the pit as usually seen is a double structure which does not at first present a direct opening from one tracheid cavity to the other, for so long as the tracheids are growing or the protoplasm is present communication between adjacent tracheids is cut off by the primary wall, which constitutes a *closing* or *pit membrane*. By a subsequent change in this latter it may eventually become displaced from its central position and then lie against one of the arches. Under such circumstances it is often not readily discernible, and the pit appears as if the primary wall had been obliterated within its limits. In the



last instance, when the active protoplasm is withdrawn and the cell passes into a permanent condition, the membrane disappears, and the pit then forms a lenticular cavity in the line of the cell wall, which opens into adjacent tracheids. This is the appearance presented by all fully developed wood of the Coniferæ. The obvious purpose of such pits is to provide channels of communication between adjacent tracheids which would otherwise be completely isolated by the impervious nature of the secondary wall. This fact serves to explain the situation in which such pits occur.

*Radial walls.* The characteristic situation of the bordered pits is on the radial walls, where, as was shown many years since (13, 160), "the pits of contiguous tracheids always correspond to one another in such a way that on each limiting surface all the cavities of the pits of one fit exactly over those of the other. The plano-convex cavities are thus applied to one another in pairs so as to form the lens-shaped pit cavities," as seen in tangential section. But on surfaces abutting on elements of another order, e.g. parenchyma cells, the bordered pits of the tracheids correspond to nonbordered pits or else are opposite an unpitted wall. Four typical variations of the bordered pits may be recognized, — (1) the multiseriate, when they are disposed in any number of rows more than two, (2) the two-seriate, (3) the one-seriate with occasional pairs of pits, and (4) the strictly one-seriate. The general sequence thus presented will be found to be in direct accord with the evolution of higher types of structure and organization.

The most primitive type of Gymnosperm presenting a multiseriate arrangement is the genus *Cordaite*s. Among eleven species of this genus which have been critically studied within recent years (45) there is a general agreement in the constancy of this character which thereby becomes of generic value. In all the species the pits are disposed in such a compact manner throughout the entire extent of the tracheid as to present a hexagonal outline. In *Cordaite*s *acadianum* they are two- to five-seriate (plate 7). In other species they vary from two-seriate in *C. hamiltonense* and *C. Newberryi* (plate 8) to occasionally

four-seriate in *C. Clarkei*. In the majority of species the rows are not constant, but show a varying number from one to three, or two to five, this variation being exhibited by adjacent tracheids in accordance with the variation of the latter in radial diameter; and viewing this distribution as a whole, it cannot be doubted that it represents corresponding differences in development. One of the most striking features of the genus is to be met with in *C. Newberryi* (plate 8), which is unique in the segregation of the pits into groups of six to thirteen.

In *Araucarioxylon* (28, 614), while conforming to the characteristic form and compact arrangement presented in *Cordaites*, the pits exhibit far less constancy in their serial arrangement, and in this respect they are at once comparable with those of the existing *Araucarias*. Among the latter *A. Cunninghamii* shows a one- to three-seriate disposition, *A. excelsa* is one- to two-seriate, while *A. Bidwillii* is strictly one-seriate. All of the extinct species as comprised in the genus *Araucarioxylon* not only show similar variations, but such variations are found to cover a much wider range. A comparison of all the species, both recent and extinct, now available for that purpose is of interest in this connection.

	1-SERiate	2-SERiate	3-SERiate	4-SERiate
<i>A. Bidwillii</i> <sup>1</sup> . . . . .	×			
<i>wurtembergianum</i> . . . . .	×			
<i>Schmidianum</i> . . . . .	×			
<i>hugelianum</i> . . . . .	×			
<i>excelsa</i> <sup>1</sup> . . . . .		×		
<i>arizonicum</i> . . . . .		×		
<i>Edvardianum</i> . . . . .		×		
<i>virginianum</i> . . . . .		×		
<i>Doeringii</i> . . . . .		×		
<i>subtile</i> . . . . .		×		
<i>argilliacola</i> . . . . .			×	
<i>Heerii</i> . . . . .			×	
<i>Cunninghamii</i> <sup>1</sup> . . . . .			×	
<i>Robertianum</i> . . . . .				×

<sup>1</sup> Existing species.

Such a comparison brings into strong relief the fact that the *Araucarias*, both past and present, constitute a transitional group with a somewhat wide range of variations, and in this respect they may be said to stand between the more stable *Cordaites* and *Dammara* on the one hand, and the far more variable *Coniferae* on the other, since in *Dammara australis* we find essentially the same features of structure and distribution as in *Cordaites*, the pits being one- to three-seriate. The sequence presented above may be held to be in the inverse order of development, and *A. Robertianum* must therefore be held to represent the most primitive form.

It is apparent that in *Cordaites*, *Araucaria* (including *Araucarioxylon*), and *Dammara* the pits are invariably distinguished by two constant features, — (1) their hexagonal form, and (2) their very compact disposition throughout the entire extent of the tracheid. They often deviate from the multiseriate arrangement typical of the group as a whole in that in individual cases they are reduced to a one-seriate arrangement. They thus tend to overlap the next group, which is distinguished by a two-seriate disposition, but any confusion which might arise from this cause may be overcome by reference to the special form and disposition of the pits, as will more fully appear in the following lines.

Among the remaining *Coniferales* twenty species of various genera, or 17.2 per cent in all, show a two-seriate arrangement, and to this group we must also add the *Gingkoales* and various fossil species. Here the multiseriate disposition of the pits involves features which at once distinguish the group as a whole from the preceding, clearly placing it upon a higher plane of development. The pits are never hexagonal but are generally elliptical or round, while they also show a strong tendency to extreme segregation. When brought into a compact arrangement, as in *Cupressoxylon*, *Sequoia*, or various species of *Pinus*, they are flattened only along the lines of limited contact, which are usually confined to one end of the pit (fig. 8). A very characteristic feature of this group is the further fact that the two-seriate arrangement is not constant, either in the same section or in the same tracheid. Both *Pinus*

*tæda* and *P. cubensis*, as also *Larix americana* and *Tsuga canadensis*, afford illustrations that, while typically two-seriate, a given section may show a strictly one-seriate arrangement, and this difference also obtains as between contiguous cells. In all such cases examination will show that the variation is directly related to the relative size of the tracheids in such a way that the narrower tracheids, or those arising from a less vigorous growth, are one-seriate. Within the individual tracheid there is

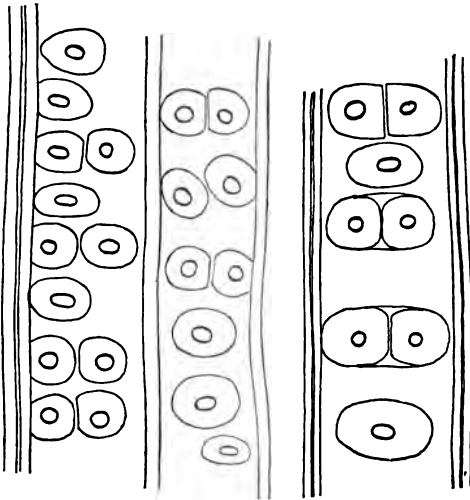


FIG. 8. *PINUS CUBENSIS*. Radial section showing the form and disposition of the bordered pits.  $\times 280$

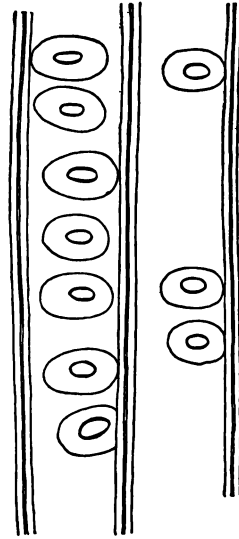


FIG. 9. *PINUS STROBUS*. Radial section showing the form and disposition of the bordered pits.  $\times 280$

a strong tendency to a one-seriate arrangement in the central region, while it is two-seriate at the extremities; and this law holds so true that in those species which are exceptionally two-seriate judgment should be reserved until it is seen that the one-seriate form holds throughout.

The antithesis of the multiserial type is found in the one-seriate form. This is typical of 50 per cent of all the species included in the present studies. In such cases the form of the pit is never hexagonal or specially flattened. When the disposition is somewhat compact, as in *Pinus strobus* (fig. 9), the outline

becomes more or less strongly elliptical, but as the segregation is more pronounced a definitely circular form prevails (fig. 10). Within the limits of the individual tracheid the same law of distribution obtains as in the two-seriate type, whereby segregation is always most pronounced in the central region.

Between species of the strictly one-seriate and those of the strictly two-seriate type there is an intermediate or transition group comprising thirty-four species, or 29.3 per cent of the investigated species, into which members of the other two groups

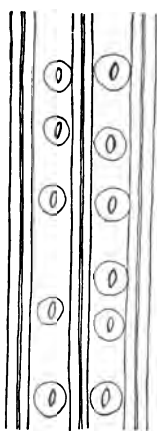


FIG. 10. *PINUS STROBUS*. Radial section showing the bordered pits of the summer wood.  $\times 280$

may occasionally be projected. The distinguishing feature of this group is the occurrence of pits in pairs, which are usually distant and in no case so numerous as to distinguish a two-seriate disposition. They give undoubted proof of the passage from one type to the other. Like the two-seriate type, this feature is not confined to any one genus or to any particular group of genera, but it applies with equal force to any genus, the members of which may therefore represent any or all of the three types here specified.

Viewing the distribution of the bordered pits from the standpoint of zonal development, it is found to be universally true that in the earlier spring wood there is the strongest tendency to a multiseriate arrangement. With a radial increase of the xylem this tendency constantly diminishes, with the general result that the pits become more strictly one-seriate and more distant toward the summer wood in which they are sometimes wholly obliterated, this being the case when the cell wall acquires unusual thickness.

Upon careful examination the foregoing facts will be found to be in exact accord with the law formulated by De Bary with reference to variations in the structure of spiral tracheids and the genesis of bordered pits, as already stated. In accordance with this law it is possible to conclude that relatively rapid

growth is coördinated with a primitive development, while the converse is true of a slow rate of growth which is again convertible into terms of maturity. On this basis we may present the following general outline of sequence in development, as preliminary to further and more detailed discussion of phylogeny:

Cordaitea . . . . .	2-5 seriate, hexagonal pits	} Compact throughout the tracheid.
Araucarioxylon . . . . .	1-4 seriate, hexagonal pits	
Araucaria . . . . .	1-3 seriate, hexagonal pits	
Dammara . . . . .	1-3 seriate, hexagonal pits	
Gingko . . . . .	1-2 seriate, round or oval pits	} More or less, often strongly, segregated.
Higher Coniferales, 1-2 seriate, round or oval pits		
Higher Coniferales, 1-seriate and pairs, round or oval pits		
Higher Coniferales, 1-seriate, round or oval pits		

*Tangential walls.* The occurrence of bordered pits in the tangential walls is a well-known and characteristic feature of the Coniferæ. In the case of fossil forms, to which *Araucarioxylon* offers a partial exception, they cannot be satisfactorily demonstrated because of the peculiar alterations of the cell wall, but that they are present we are permitted to infer from analogy with existing species upon which dependence must be placed for an elucidation of the general law. The typical position for such pits is upon the tangential walls of the summer wood, where they are seen most satisfactorily in radial section, inasmuch as they are always readily observable when present, and their most essential features are displayed in a manner not possible in a tangential section (fig. 11).

This position obviously results because of limitation of the radial walls through radial compression. The pits are therefore always confined to the few outermost tracheids of the last-formed summer wood, and in some cases they are confined exclusively to the last tracheid.

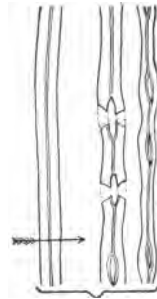


FIG. 11. *SEQUOIA GIGANTEA*. Radial section showing bordered pits in the tangential walls of the summer wood.  $\times 280$

Pits occur in this position in 71.7 per cent of all the investigated species, and their absence in 28.3 per cent points to some special features in development which may be assumed to have a general bearing upon the questions of descent and relationship. In *Dammara*, as represented by the one species *D. australis*, such pits are a prominent and characteristic feature, but in the nearly related *Araucaria* they are remarkable for their uniform absence. In the primitive *Gingkoales* they are also present, but among the *Taxaceæ*, while generally present, they are occasionally wanting, as in *Torreya taxifolia* and *T. nucifera*, or in 66.6 per cent of the investigated species of that genus. Nowhere else among the *Coniferales* do we find such a feature until we reach the genus *Pinus*, the second and higher section of which is almost invariably characterized by their absence, thus presenting an exceptional feature to the extent of 68.3 per cent of that genus. That such absence represents a process of obliteration conformable to De Bary's law cannot be doubted, while the sporadic recurrence of this feature in often widely separated genera, or in particular species of a given genus, must be held to have a more or less direct bearing upon the general course of development. This is emphasized by the observation that in *Larix americana* and *L. leptolepis*, as also in *Picea bicolor*, there is a more or less pronounced tendency to an obliteration which is never fully developed. This is expressed in the somewhat remote position of the pits and their very small size, which renders them obscure and often difficult to discover. In this respect these species represent transitional forms.

As an exceptional feature bordered pits may sometimes be found upon the tangential walls of the spring wood. This is especially noticeable at the ends of tracheids, and in rare cases it may apply to the entire extent of the wall. The most notable instance of this kind, because practically unique, is to be met with in *Sequoia gigantea* (figs. 12 and 13). Those spring tracheids which lie in direct contact with the summer wood of the previous year often exhibit this feature with great prominence, but it may also extend radially through several successive tracheids.

This is undoubtedly a primitive character, and in the one case cited it possesses some value for the purpose of specific differentiation, but in general terms the occurrence of bordered pits in such positions is of so sporadic a nature as to give this feature no well-defined value, either for taxonomic or phylogenetic purposes. It may, nevertheless, be stated with respect to the pits on the tangential walls of the tracheids in general, that in their distribution they distinctly conform to the law governing similar structures on the radial walls.

Reference to *Cordaites acadianum* shows that in the multiseriate pits of the hexagonal form these structures always preserve the

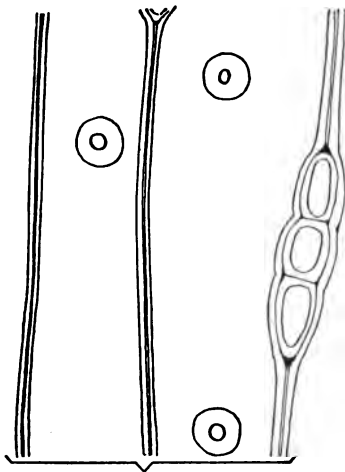


FIG. 13. *SEQUOIA GIGANTEA*. Tangential section showing bordered pits in the tangential walls of the spring wood.  $\times 280$

spiral arrangement characteristic of the structures from which they were derived (plates 3-6), and this conformity also extends to the

direction of the spirals which generally ascend from left to right. The general law in this respect has already been formulated so fully by De Bary (13, 163) as to make it unnecessary at this time to enter upon its consideration more in detail, beyond a reference to one

or two special features and some apparently exceptional cases. While the spiral arrangement is always typical in such genera as *Cordaites*, *Dammara*, *Araucaria*, etc., it is not obvious in those cases where the pits are strictly one-seriate and often remote

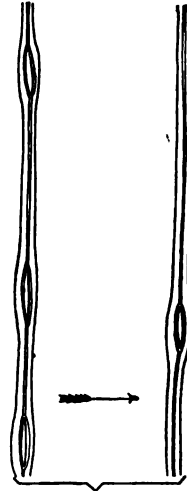


FIG. 12. *SEQUOIA GIGANTEA*. Radial section showing the bordered pits on the tangential walls of the spring wood.  $\times 280$



from one another. Nor is it apparent at first sight in those cases of two-seriate pits where, as in *Cupressoxylon Dawsoni* from the Cretaceous, *Larix americana*, *Sequoia*, and various species of *Pinus*, the pits are always paired off in such a way that the axis of each pair is at right angles to the axis of the cell (fig. 8). Two explanations are here possible: (1) the spirals are in reality two-seriate, and are projected through the alternate members of the two rows of pits; or (2) the disposition of the pits represents an extreme phase in the flattening of

the original spirals conformably to a higher type of development. This view, which seems the more reasonable, is in direct harmony with De Bary's law, while it receives additional support from the form and direction of the pit orifice.



FIG. 14. *PINUS PUNGENS*. Bordered pits on the radial walls of the summer wood.  $\times 280$

The orifice of the pit is variable, at different times being round, when the pits are also round and more or less distant; oval or oblong, when the pits assume corresponding forms; or, in the summer wood, lenticular or oblong. The transversely elliptical pits of *Pinus strobus* (fig. 9), the orifice of which is also transversely oblong, as also the similar pits of *Pinus cubensis* (fig. 8), afford substantial proof in confirmation of the probable correctness of this view. In the summer wood the pit orifice commonly assumes a position which appears to

offer a direct contradiction to this conclusion. In *Pinus strobus* (fig. 10) the orifice is oblong and parallel with the tracheid axis. In *Pinus pungens*, as in many others of the same genus (fig. 14), the narrow orifice is extended above and below into a diagonal slit of great length, forming a narrow angle with the tracheid axis. At first sight this would seem to imply that these features represent primitive spirals, the original direction of which has not been greatly if at all modified, but one or two considerations will assist us to a correct interpretation of this feature. In the

first place, it is to be observed that such positions and modifications of the orifice are invariably associated with the summer wood; if they occur in the spring wood, it is the result of maceration and commonly appears in fossil plants or woods in process of decay, and they are always most conspicuous in those tracheids which have experienced the most profound modifications with respect to the growth in thickness of the secondary walls. It has already been shown in the case of *Taxus* and *Torreya* that there is no necessary connection between the spiral bands and the spiral lines of striation, — that, as a matter of fact, as particularly illustrated by *Torreya taxifolia*, the two are quite distinct from one another under ordinary conditions of development; but in cases where the wall experiences extreme growth in thickness the obliteration of the original spiral structure is complete, and at the same time it is replaced by the normal striation of the wall, which then becomes most pronounced. Instances such as those afforded by *Pinus strobus* and *P. insignis* may, according to this interpretation, be held to represent the final phases in the obliteration of the original spirals, and they therefore constitute characters indicative of the highest type of development. In a few cases the structure of the bordered pit presents exceptional forms. In *Cupressus nootkatensis* the pit orifice shows either unusual want of regularity in outline and marked eccentricity of position, or it is so enlarged as to leave only a narrow border to the round or oval pit (fig. 15). Similar features occur occasionally in other genera, and they are generally conspicuous in *Pinus tæda*. De Bary has directed attention to the same feature in *Ephedra* (13, 159) and *Pinus sylvestris*, and he correctly interprets it as a form of arrested development. Alterations also arise as a feature of

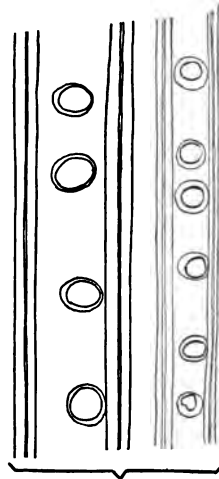


FIG. 15. *CUPRESSUS NOOTKATENSIS*. Radial section showing deformed bordered pits.  $\times 280$

secondary growth in those cases in which the wall acquires unusual thickness. This is typically the case in *Pinus cubensis*, where in plan (fig. 16) the orifice is extended



FIG. 16. *PINUS CUBENSIS*. Radial section showing deformed bordered pits.  $\times 280$

vertically to a length often twice the diameter of the original pit. In tangential section, according to the particular direction of the plane of section (fig. 17), the orifice is either of uniform width or it enlarges constantly through the entire thickness of the later growth, from within outwards. That such unusual

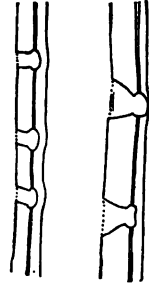


FIG. 17. *PINUS CUBENSIS*. Tangential section of bordered pits as in fig. 16.  $\times 280$

forms are features of extreme secondary growth of the wall, and that they may be anticipated in all cases where such modifications of the walls occur, is a reasonable deduction from the observed facts.

#### BORDERED PITS — TAXONOMIC AND PHYLOGENETIC

For taxonomic purposes the bordered pits possess a definite though often limited value. In the genus *Cordaitea*, as also in *Araucarioxylon*, *Araucaria*, and *Dammara*, this is expressed in the hexagonal form together with their very compact, chiefly multiseriate arrangement throughout the entire extent of the tracheids, — characters which are of generic value and at once serve to separate these genera from all others. The contrasting differential feature is then to be found in the pits of the oval or round form, together with their two-seriate or one-seriate disposition, with a more or less marked tendency to segregation. This is characteristic of the *Ginkgoales* and all the *Coniferales*, both fossil and recent.

As a differential character of subgeneric value, the occurrence of bordered pits on the tangential walls of the summer wood of

the first section of *Pinus* (the soft pines) and their almost invariable absence from the same structural region in the second section (the hard pines) is one which may be always relied upon.

For the purposes of specific differentiations the pits on the tangential walls possess a distinctly inferior value, which must be confirmed in most cases by the evidence of other factors. Their utility in this respect is made sufficiently clear in the various diagnoses and in the artificial key, without further discussion at this time.

In the genus *Cordaites*, according to the provisional specific differentiations of fossil forms as at present generally employed, the number of rows of pits, or their segregation into definite groups, are characters of well-defined specific value, since they are among the few features which may be utilized with certainty for this purpose. Thus *C. acadianum* with its two to five rows, *C. materiarium* with two, rarely three to four, rows, *C. hamiltonense* with two rows, and *C. Newberryi* with two rows, in groups of six to thirteen pits, rest upon a basis which is not only easy of recognition but which may be applied with full assurance. In *Araucaria* the three species investigated may be similarly differentiated from one another. The same rule is applicable to *Torreya taxifolia*, which is thereby separable from the other species; likewise to *Cupressoxydon Dawsoni*, *Tsuga canadensis*, and *Larix americana*, and, among the pines, to *P. Lambertiana*, *P. clausa*, *P. Sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis*. It is to be observed, however, that the constancy which characterizes this feature in *Cordaites* and *Araucaria* is wanting in the higher *Abietineæ*. In *Larix* there is such variation that very careful scrutiny is required, while in the genus *Pinus* the number of exceptions to the typical character increases greatly and is liable to cause some difficulty in the final determinations unless much care is exercised. *Pinus tæda* offers a conspicuous illustration of this fact, as may be seen by reference to the analytical key. It is therefore manifest that the value of the bordered pit for taxonomic purposes is most clearly defined in the lower types of the *Coniferales*, and that their value diminishes steadily with

an advance towards higher forms of organization and development. In all cases where exceptional forms introduce diagnostic difficulties these may be overcome by the controlling effect of associated characters.

We are now in a position to examine the data at hand with a view to determining the bearing of the bordered pits upon questions of phylogeny.

Having reference to the origin of the bordered pit and the various modifications it presents in the course of development, it cannot be doubted that the hexagonal, multiseriate pits of *Cordaite*s, *Araucarioxylon*, *Araucaria*, and *Dammara* place these genera in a relatively inferior position, — a view which gains a large measure of support from the well-known and extensively multiseriate disposition shown in *Heterangium Grievii* (81, 341), but the facts so far discussed have not as yet thrown any special light upon the relative positions of the separate genera.

An examination of twelve species of *Cordaite*s shows that the bordered pits exhibit a much wider range of serial variation than any other genus covered by the present studies. If then we accept the general principle with respect to the development of the bordered pits as already illustrated, it cannot be doubted that the two- to five-seriate pits stand much nearer to the primitive form of the tracheid than do the one-seriate. From this point of view it is then evident that in *C. recentium*, the name of which is thereby seen to be fully justified, the one-seriate pits place it at the upper end of a series which has its inferior termination in the two- to five-seriate *C. acadianum*, while intermediate forms appear between the two as members of a series of nine variants, and it is possible to arrange these in such a manner as to exhibit the probable sequence in development, as seen by table on the following page.

The wide range of variations here shown, especially when compared with other genera, at once serves to suggest that *Cordaite*s was in this respect somewhat of the nature of a transition group from which others were given off, or else that it epitomized the collective changes through which a number of

genera must have passed. And inasmuch as this genus exhibits a more highly developed multiseriate arrangement than any other within the general phylum, we must concede that it is, with respect to this character, the most primitive of all.

SERIAL VARIATIONS IN THE BORDERED PITS OF CORDAITES

	2-5 SERIATE	3-4 RARELY 2	2-4 CHIEFLY 3	3-4 CHIEFLY 2	2-3 RARELY 4	2-3 CHIEFLY 2	1-3 CHIEFLY 2	2-SERIATE	1-SERIATE
<i>C. acadianum</i> . . . . .	×								
<i>ohioense</i> . . . . .		×							
<i>ouangondianum</i> . . . . .			×						
<i>materiarium</i> . . . . .				×					
<i>Clarkei</i> . . . . .					×				
<i>annulatum</i> . . . . .						×			
<i>Brandlingii</i> . . . . .							×		
<i>materioide</i> . . . . .							×		
<i>illinoisense</i> . . . . .							×		
<i>hamiltonense</i> . . . . .								×	
<i>Newberryi</i> . . . . .								×	
<i>recentium</i> . . . . .									×

The genus *Araucaria* shows a much more restricted range of variations, there being only four variants pretty uniformly distributed among fourteen species, both recent and fossil (*ante*, p. 61). While the most highly developed members, four in number, are represented by one-seriate pits, the most primitive form of four-seriate pits occurs in only one case, — *A. Robertianum*. It is therefore manifest that this genus is obviously of a more advanced type than *Cordaites*, from which it undoubtedly originated. *Dammara* being represented by only one species, it is not possible to locate it more definitely than to say that the one-to three-seriate disposition of its pits would place it in a position equivalent to that occupied by *Araucaria Cunninghamii*, and therefore about three fourths of the way down the scale for that genus. This fact points with much force to the idea that of the two genera *Dammara* is of relatively lower type.

The Ginkgoales and the Coniferales as a whole exhibit an obviously higher type of development than the preceding group, in consequence of the more pronounced tendency to segregation of the pits, which are now either elliptical or round, and never hexagonal. This distinction is so clearly defined and constant as to support the idea, which gains force in other ways, that Cordaites, Araucaria, and Dammara are clearly related members of a principal branch of the original stock, and that they therefore diverge considerably from the particular line of descent within which we find both the Ginkgoales and the Coniferales.

Ginkgo, being the unique representative of an ancient line, cannot very well be brought into the present discussion very much in detail. On other grounds it is known to be a primitive form representing a group distinctly inferior to the Coniferales, and this view is supported by the disposition of the pits in two series, a character which, if taken alone, would give the genus rank with *Torreya taxifolia* among the Taxaceæ, but when regarded collectively would place the genus distinctly below the Coniferales as a whole. This evidence, then, indicates that the Ginkgoales must have arisen as a side line at some point inferior to the Coniferales but superior to the Cordaitales.

In the Taxaceæ the bordered pits do not in themselves afford very conclusive evidence as to the relative position of the family. Among the eight investigated species, representative of three genera, only three, and chiefly two, variants occur. Taken alone, the disposition of the pits would lead to no final conclusion, but other factors permit of placing this family in the inferior position usually assigned to it. In the genus three variants are found,—the one-to-two rows of *T. taxifolia*, the one row or pairs of *T. californica*, and the strictly one-seriate form of *T. nucifera*. In *Taxus* only two variants appear,—the one row or pairs of *T. floridana* and the one-seriate disposition as found in the remaining three species. The one representative of *Podocarpus* shows but one variant, and that is one-seriate. From this it is obvious that the generic sequence must be in the order

given, and that the sequence of species must be approximately as given in the table of anatomical data.<sup>1</sup>

The observations so far made apply altogether to the pits on the radial walls. We may now pass to a consideration of their relation to the tangential walls, a factor which does not call for very extended discussion. This feature is found to apply to 71.7 per cent of all investigated species exclusive of fossils. It is wanting in three species of *Araucaria*, representing 2.58 per cent; in two species of *Torreya*, or 1.72 per cent; and in the entire second section of *Pinus* to the extent of twenty-eight species, or 24.1 per cent. But the occurrence of pits on the tangential walls, in common with those on the radial walls, is a well-known feature of the *Sigillarias* (81, 198), where their primitive character is well established, and we can hardly doubt that their final elimination in the higher pines is the expression of a final phase in development consistent with the position usually assigned those plants.

The absence of pits from the tangential walls of certain *Araucarias* and *Torreya*s is to be interpreted as one of those sporadic tendencies toward a higher type of development which never become permanent in the same line, but which are to be met with as one of the invariable features of evolution.

The remaining genera of the *Coniferales* present so few deviations from a typical form that they cannot be differentiated fully on the basis of the bordered pits. This character nevertheless has a definite value in association with others, as in the genus *Sequoia* or some of the hard pines, *Larix americana*, etc. The general sequence of genera may be recognized by the bordered pits only in so far as these structures serve to confirm and emphasize the conclusions reached in other ways, and this will become apparent from an inspection of the table already referred to. It will nevertheless serve a useful purpose at the present moment to ascertain the general sequence based upon the percentage distribution of the principal variants, as seen by the table on following page.

<sup>1</sup> Appendix A.



COMPARISON OF THE PRINCIPAL VARIATIONS IN THE SERIAL ARRANGEMENT OF BORDERED PITS, BY PERCENTAGES

	TOTAL VARIATIONS	2-5	2-4	2-3	1-3	2	1-2	1+ PAIRS	1
Cordaitea . .	9	8.3	25.0	16.6	25.0	16.6			8.3
Dammara . .	1		6.6	20.0			40.0		33.3
Araucaria . .	4		6.6	20.0			40.0		33.3
Ginkgo . . .	1						100.0		
Sequoia . . .	1						100.0		
Larix . . . .	3						33.3	33.3	33.3
Taxodium . .	2						25.0		75.0
Libocedrus .	1							100.0	
Thuja . . . .	1							100.0	
Pseudotsuga .	2							50.0	50.0
Pinus . . . .	3						17.1	41.5	41.4
Abies . . . .	3						13.6	27.3	59.1
Taxus . . . .	2							25.0	75.0
Tsuga . . . .	3						16.7	16.7	66.6
Picea . . . .	2							10.0	90.0
Podocarpus .	1								100.0
Thujopsis . .	1								100.0
Cryptomeria .	1								100.0

With respect to specific differentiations it has already appeared that the bordered pits may be employed with success in *Taxus* and *Torreya*. In *Cupressus* this rule also applies to *C. pisifera* and *C. macrocarpa*, both of which are distinguished by having their pits in one row or pairs, while the remaining seven species have strictly one-seriate pits. An instructive example is afforded by *Cupressoxylon Dawsoni*. In this species, which is of early Tertiary age (Lignite Tertiary), the pits are typically two-seriate, being disposed in a very compact manner similar to that found in existing *Sequoias*. But in a series of eleven specimens it is clearly seen that two variants are represented, the second being a one-seriate form. These variations are also found, as in the other Coniferales, to be directly related to variations in the size and rate of growth of the tracheid. It cannot be doubted, then, that *C. Dawsoni* is a more primitive

representative than any species now existing, and that it is substantially the ancestral form of the genus, so far as we know.

In *Larix* the four investigated species may be differentiated pretty fully, and this rule applies with particular force to *L. americana* and *L. occidentalis*, both of which are distinguished by two-seriate forms. Among the pines *P. Lambertiana*, *P. clausa*, *P. Sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis* are readily differentiated from the others by the two-seriate pits. In all other cases than those specifically indicated the bordered pits afford an inadequate basis for specific differentiation.

It is now apparent that segregated round or oval pits in one row must be taken as representing the highest type of development in the Coniferales, and any deviation from this must be taken to indicate the survival of more primitive conditions, pointing to derivation from a type like that of *Araucaria* or *Cordaite*s. From this point of view the occurrence of pits in one-to-two rows in *Larix americana*, *Torreya taxifolia*, *Sequoia*, *Tsuga canadensis*, and various species of *Pinus* indicates the survival of ancestral characters which are partial to the extent of 7.2 per cent, and complete to the extent of 10.8 per cent. That such deviations from the usual type of structure are either survivals or reversions which serve to indicate a common origin cannot be doubted, more especially as they do not occur at a fixed point near the original type, but they arise sporadically in widely separated genera. The tendency of such evidence, then, is to show a common ancestry for the various genera of the Taxaceæ and Coniferæ, a view which is greatly strengthened by the testimony afforded by the spiral tracheids of *Larix americana*, *Pseudotsuga*, and *Pinus tæda*.

## CHAPTER V

### MEDULLARY RAYS

#### GENERAL STRUCTURE

The medullary ray, in the various details of its structure, as presented radially and tangentially, comprises some of the most important features for diagnostic and taxonomic purposes. While it presents numerous variations, these are, in the main, of such a nature as to give them very positive value for both generic and specific differentiations. Primarily the medullary rays are to be regarded as a residue of the original fundamental structure, which has been left over in the genesis of the primary stele, but they are capable of reproduction or extension under the influence of the cambium in the course of secondary growth. In all such cases, however, they are typically composed of the same elements which are necessarily *parenchymatous*. Deviations from this structure may appear through the introduction of other elements, but such alterations always arise in a manner which indicates their relation to the evolution of higher types of organization.

In a transverse section the medullary ray appears usually as a simple, radial series of elongated cells with transverse terminations. Deviations from this type of structure occur only in the case of the rather rare two-seriate forms, which appear in the transverse plane of section only at wide intervals, or in the case of rays which contain resin passages, as in *Picea*, *Pinus*, *Larix*, etc., when the structure presents a varying aspect dependent upon the particular plane of section. In *Pinus reflexa* the side walls of the ray cells may be seen projecting into the cavities of adjacent tracheids, where they form short, saclike bodies of the general nature of thyloses, which they really

are (fig. 18). Such a feature is of specific value in differentiation. With this exception the ray presents no features in this plane of section which merit special consideration.

*Radial section.* Viewed radially, the medullary ray is seen to be composed of a series of cells extended in a radial direction and superimposed so as to form a muriform band from one to many cells in height. In general terms, the higher the ray the lower the component elements, from which it follows that in one-celled rays the cells are usually highest; but this feature is only of general interest, since it rarely has a bearing upon the chief questions at issue. In some cases two structural types may be recognized, — the one containing resin passages, the other devoid of such structures. Where such passages occur the structure of the ray shows a variation of detail which makes it of no value for diagnostic purposes, and the relation is one which possesses interest only in so far as it applies to the distribution of the resin passages themselves.

A feature of primary importance in the constitution of the ray is the occurrence of two kinds of parenchyma cells. In 95 per cent of the genera the upper and lower walls are always thickened by secondary growth and more or less strongly perforated by simple pits (figs. 19 *b*, 25, and 27).

This feature also applies to 56.1 per cent of the genus *Pinus*. It possesses no special value for either specific or generic differentiations except so far as it applies to cells which are markedly different and justify the special terms *thick walled* and *thin walled*. It is obvious, then, that the thick-walled cell is to be regarded as the normal structure for the ray of the Coniferales as a whole, while the thin-walled represents the exceptional form which is introduced in response to some special demands. Although the

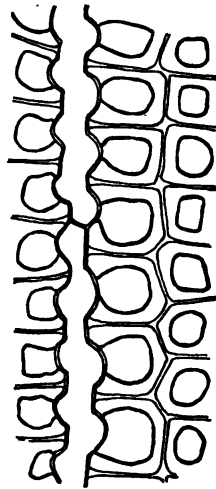


FIG. 18. *PINUS REFLEXA*. Transverse section of a medullary ray showing the inflation of the cells opposite tracheids.  $\times 300$

thick-walled cells occur in the genus *Pinus* to the extent of 56 per cent, they show a diminishing frequency, eventually becoming rare and are ultimately replaced by thin-walled cells. Reference to them in the following diagnoses is always specified by (1). In 43.9 per cent of the genus the upper and lower walls are thin and absolutely devoid of pits. For diagnostic purposes such cells are always referred to as (2). In some cases they are so undeveloped as to be obscure and readily broken out in the process of section

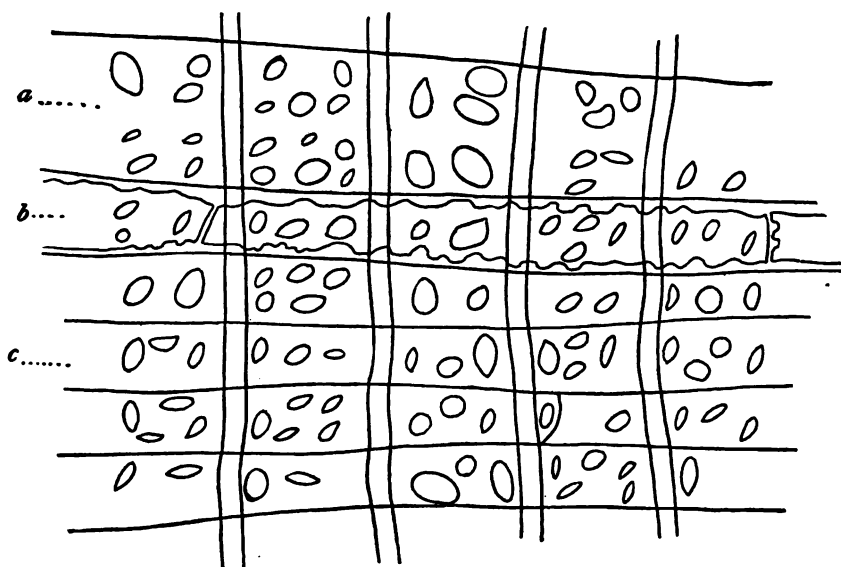


FIG. 19. *PINUS PALUSTRIS*. Radial section of a medullary ray showing characteristic pits on the lateral walls: *a*, a thin wall broken out; *b*, thick-walled parenchyma; *c*, thin-walled parenchyma.  $\times 280$

cutting, so that they are often entirely wanting (fig. 19, *a-c*). Such thin-walled cells are typically developed in *P. palustris*, *P. taeda*, etc., and it is to be observed that they are always associated with the highest forms of development. Transition forms occur. These are first seen in the soft pines, where occasional thin-walled cells devoid of pits are interspersed and are often conterminous with the thick-walled elements. In the hard pines the same relation exists, but it is gradually reversed until the

thin-walled cells altogether predominate. Such gradations are exhibited in *P. Coulteri*, *P. Jeffreyi*, *P. pungens*, *P. tæda*, *P. cubensis*, and *P. inops*, and they afford valuable evidence as to the sequence in development of the species. In *P. Murrayana*, *P. cubensis*, and *P. insignis* the transition forms exhibit much more detailed gradations, by virtue of which it is often exceedingly difficult to distinguish between the two forms of cell, since whether conterminous or parallel the variations in thickness

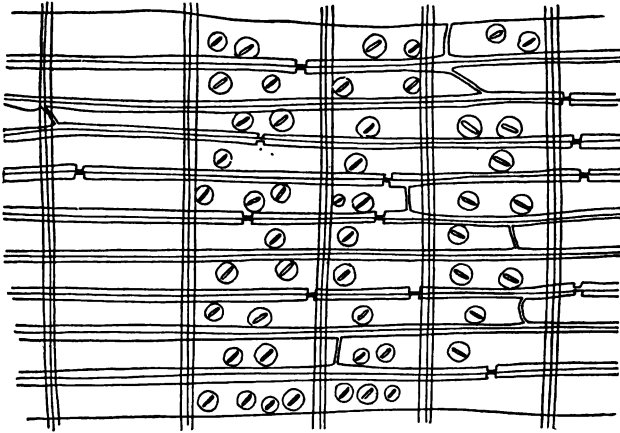


FIG. 20. *TAXODIUM DISTICHUM*. Medullary ray showing the structure and position of the pits on the lateral walls; the straight ray cells and the thin, straight, terminal walls.  $\times 280$

change in such a way that the one type passes gradually into the other. When these variations are viewed collectively and taken together with the general fact that the thin-walled cells are a feature of the higher types of organization, we may reasonably conclude that the thin-walled cells have been derived from the thick-walled through a process of arrested development. The cause of such alterations is to be sought for, and it will doubtless be found in connection with another component of the ray.

The terminal walls of the ray cells present three typical variations, — (1) thin-walled and entire, (2) thin-walled and locally thickened, and (3) thick-walled and coarsely pitted.<sup>1</sup> The first

<sup>1</sup> See Appendix A.

feature is a characteristic of 52.6 per cent of all the genera, inclusive of *Ginkgo*, from *Dammara* to *Sequoia*, while it also appears in *Cupressus* and *Abies* in part as exceptional, and in the genus *Pinus* to the extent of 85.3 per cent. The wall presents no secondary growth in thickness, either locally or generally. In the majority of cases it crosses the line of the principal cell axis either at right angles or diagonally, — features which are usually of very secondary value, although in a few cases, as *Taxodium*, it may serve a useful purpose as an associated character for differentiation from closely allied genera (fig. 20). In other cases the wall is more or less strongly curved. This feature is prominent in *Thuja*,

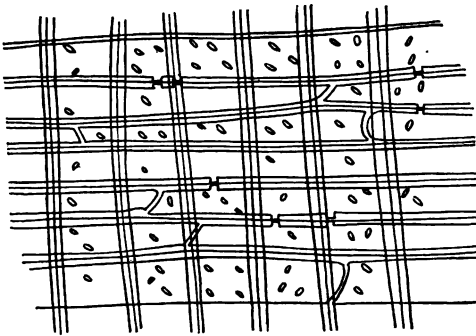


FIG. 21. *THUYA GIGANTEA*. Medullary ray showing the form and disposition of the pits on the lateral walls; the thin and curved terminal walls; the cells contracted at the ends.  $\times 280$

*Cupressus*, *Podocarpus*, *Thujopsis*, and *Cryptomeria*, as also in the more highly developed hard pines. To a less extent it also occurs in *Taxodium*, and it constitutes a character of some value for differential purposes (fig. 21).

The second variant differs from the first in that the otherwise thin wall is locally thickened (fig. 22), the secondary growth forming one or more beaded enlargements. This is a feature which occurs exceptionally in *Abies*, *Pseudotsuga*, *Picea*, and *Pinus*, but it is typical in *Cupressus* (66 per cent) and *Juniperus* (72.7 per cent), where it constitutes a diagnostic element of great value. It is in all cases, however, to be regarded as a transitional form between the first and the third variant, and from this point of view it also possesses a somewhat definite phylogenetic value. The third variant is characterized by a marked general, secondary growth of the wall, which thereby becomes more or less strongly thickened and traversed by numerous simple pits

(fig. 23). It occurs exceptionally in *Juniperus* and *Pinus*, but it is typical in *Abies* (90.9 per cent), *Tsuga* (100 per cent), *Larix* (100 per cent), and *Picea* (90 per cent). In *Abies* and *Juniperus*, where transitional forms sometimes occur, the walls in the spring

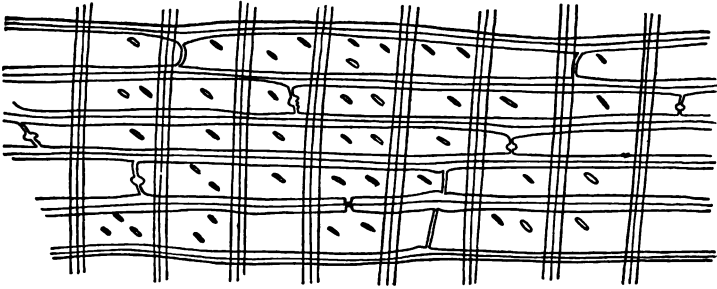


FIG. 22. *CUPRESSUS MACNABIANA*. Medullary ray showing the form and position of the pits; the thin, curved, and locally thickened terminal walls.  $\times 280$

wood may be only locally thickened, but in such cases the typical feature always appears in the summer wood, where such secondary alterations are most strongly emphasized.

For taxonomic purposes such features possess a definite value. The thick-walled cells of *Tsuga*, *Larix*, and *Picea* permit of an

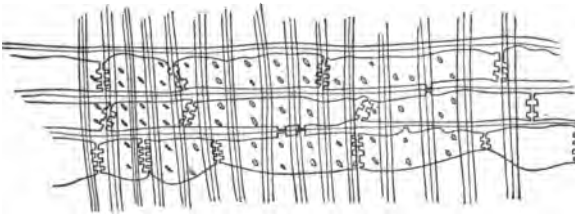


FIG. 23. *JUNIPERUS OCCIDENTALIS*. Medullary ray showing the form and disposition of the pits on the lateral walls; the thick and coarsely pitted terminal walls.  $\times 280$

easy and definite segregation of these three genera in those cases which otherwise might involve a strong element of doubt, and the same rule holds true, though to a less extent, with respect to the locally thickened walls in *Cupressus* and related genera.

Pits on the lateral walls of the ray cells are an invariable feature of all investigated species of *Ginkgoales* and *Coniferales*,



including fossil representatives and the Cordaitales. They vary very much in form, size, and number. In such types as *Juniperus* they are most diminutive (fig. 23) and generally numerous, while in many of the pines, such as *P. resinosa* or *P. koraiensis*

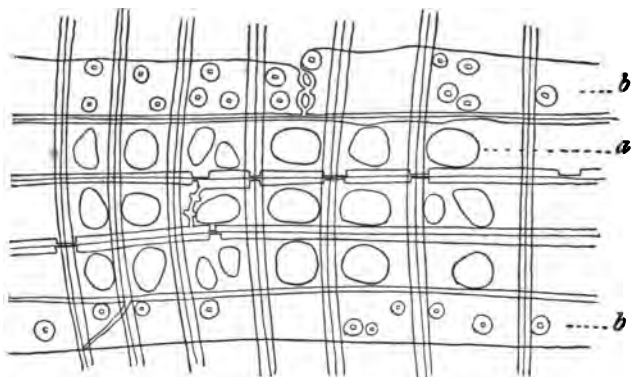


FIG. 24. *PINUS REFLEXA*. Medullary ray showing (a) the form and disposition of the pits on the lateral walls; (b) the ray tracheids.  $\times 280$

or *P. reflexa* (fig. 24), they attain to maximum size and occupy nearly the entire surface of the wall within the limits of a wood tracheid, thereby becoming few in number. In *Sequoia* (fig. 25) or *Taxodium* (fig. 20) they are typically oval, in *Pinus cubensis*

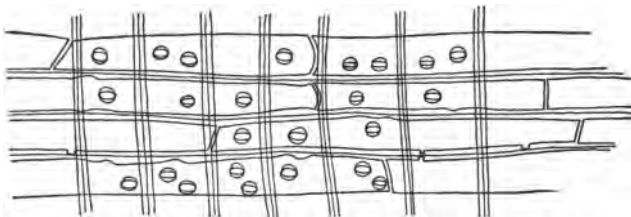


FIG. 25. *SEQUOIA GIGANTEA*. Medullary ray showing the form and disposition of the pits on the lateral walls.  $\times 280$

or *P. tæda* (fig. 26) they are variously lenticular, while in *P. resinosa* or *P. koraiensis* they are oval or oblong, or even quadrangular. Such variations as a whole are far more numerous and sharply defined in *Pinus* than in any other genus known. In all the investigated genera the pit is bordered. This finds

either partial or complete exceptions in the genus *Pinus* to the extent of 78.1 per cent of the species, in which the pits are either simple throughout or else they exhibit a more or less definite border in the summer wood only. That a border is a characteristic feature of fossil representatives is justified by comparison with existing species, but it is not always recognizable in consequence of the alterations of structure due to the general process of petrification. Such obliteration not infrequently involves the pit orifice also. It is thus apparent that such structures often fail in the determination of fossils. In existing species the border

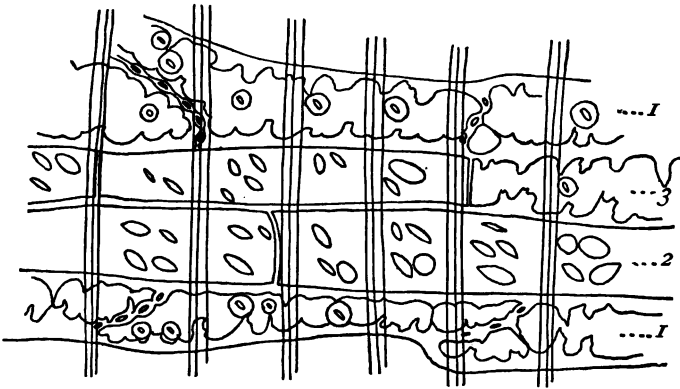


FIG. 26. *PINUS SEROTINA*. Medullary ray showing (1) the ray tracheids with dentate walls; (2) the structure of the parenchyma cells; (3) tracheids continuous with parenchyma cells.  $\times 280$

is often so faintly defined as to be difficult of recognition, and this is especially the case in rays of a resinous character. In all such cases, however, the requirements of a correct diagnosis are fully met by the pit orifice. The general law of development, then, is such that all genera except *Pinus* may be held to be characterized by bordered pits. Their strong tendency to obliteration in that genus is found to coincide with the more marked development of ray tracheids, which undoubtedly assume more completely the original functions of the parenchyma cells, these latter in consequence suffering constant structural reduction, as in the hard pines.

In the distribution of the pits an important feature appears in the numerical variation in different parts of the ray. For diagnostic purposes it is necessary to have reference to the number of pits not upon the entire surface of an individual cell but within the limits of a spring or summer tracheid, as the case may be. They are invariably most numerous in the region of the earliest spring tracheids, usually diminishing toward the summer wood, where the change may sometimes take place abruptly, and in which they are most commonly reduced to one, with occasional obliteration in the most highly modified tracheids last formed. A similar law of distribution is applicable within the vertical limits of the ray. When these structures are several cells in height the number of pits is typical, and, within certain narrow limits, constant for all except the marginal cells. Thus if the normal number is one to two for the central cells, it may sometimes rise to four, six, or eight in the marginal cells only, and such exceptions must be noted in diagnosis. When the ray is only one cell in height the number of pits agrees with that for the marginal cells. Such numerical variations possess but little value for generic purposes, but as a specific character they may be held to constitute the principal differential feature in the last analysis. These relations are expressed typically in the genus *Sequoia*, the two species of which may be definitely differentiated. *S. gigantea* is characterized by oval and commonly narrowly bordered pits, the broadly oblong orifice equal to the outer limits of the pit and chiefly parallel with the cell axis, one to two, more rarely three to four, per tracheid. In somewhat sharp and definite contrast to this, *S. sempervirens* has large, oval, narrowly bordered pits, two to six per tracheid, the round or broadly oblong orifice being either parallel with or diagonal to the cell axis. In *Libocedrus* the pits are small, narrowly bordered, oval, with a lenticular, diagonal orifice, one to four per tracheid. Or again, in *Larix americana*, the pits are "two to six per tracheid, becoming distinctly smaller toward the summer wood where they are abruptly reduced to two and finally one per tracheid." In *Cupressus pisifera* the pits are "chiefly two

in radial series, or in the marginal cells and low rays upwards of six per tracheid." In *Taxodium distichum* the pits are round, conspicuously bordered, and large, with a very narrowly lenticular and diagonal orifice, which is often as long as the outer limits of the pit. But in the analytical key it will be observed that this genus is naturally brought into close relations with *Sequoia*, which is also distinguished by large bordered pits. The ultimate differentiation then rests upon the fact that in the latter the pits are *oval*, the border often *narrow*, sometimes *obscure*, while the *oblong* or lenticular, usually rather broad, orifice is generally parallel with the cell axis. As a final illustration, the four pits of *Pinus monophylla*, or the one to five throughout, finally reduced to one to two in the summer wood of *P. Balfouriana*, point with much definiteness to these particular species, while among the hard pines the occurrence of large oval or squarish pits, one or rarely two per tracheid, segregates a group of four species. Detailed as these features are, they are not accidental, but of such constancy as to admit of no hesitation in accepting the conclusions to which they point.

The length of the ray cell is subject to considerable variation not only within the limits of an individual but also between one species and another. Our studies, however, do not permit the formulation of a law applicable to specific differentiations, even if such a law does exist, which present evidence leads us to doubt; but details of length, in terms of spring tracheids, have been incorporated in all the diagnoses, since they are often very suggestive and thus may assist in the ultimate recognition of the species.

The form of the cell is of more evident value, although too much stress must not be laid upon it. The cell is either straight, as in *Juniperus*, *Libocedrus*, or *Picea* (fig. 23), or it becomes fusiform through contraction of the extremities, as in *Cupressus*, *Sequoia*, *Taxodium*, etc. (fig. 21). As a well-defined differential character its value is only one degree higher than the length of the cell, and for the same reason it has been introduced into the diagnoses as a controlling factor of secondary importance.

## CHAPTER VI

### MEDULLARY RAYS (*continued*)

#### RAY TRACHEIDS

In the higher Coniferæ the medullary ray is distinguished by the presence of an element which differs materially in its structure from the associated parenchyma cells. These elements have been designated as *ray tracheids* (13, 491-492). Their structure is so peculiar, and they present such important relations to classification and development that a somewhat detailed account of them is necessary, to some extent in recapitulation of well-known observations (13, 461; 21, 13; 82).

As stated by De Bary, the ray tracheid resembles the parenchyma cells, from which they differ, however, in the presence of bordered pits on *all* their walls. Furthermore such pits not only differ materially in form and size from the bordered pits of adjacent parenchyma cells, but they are always much smaller than the pits of those wood tracheids on which they border. Such tracheids are invariable features of the ray in all the higher Coniferæ from *Tsuga* and *Pseudotsuga* to *Pinus*, to the extent of 25 per cent of the investigated genera. In *Juniperus* they occur very rarely, being found, so far as I am aware, in only one species (*J. nana*) out of a total of eleven, and they are so sparingly developed as to readily escape observation. In *Thuja* they are to be met with in *T. japonica*, likewise in a rudimentary state of development. Out of nine species of *Cupressus* they occur only in *C. nootkatensis*. Of the ten investigated species of *Abies* they are found only in *A. balsamea*. In commenting upon this fact many years since (13, 490), it was also pointed out that among European species *A. excelsa* is similarly exceptional, but no attempt has been made to interpret the significance of such facts.

In *Thuja*, *Cupressus*, and *Abies* the tracheids are strictly marginal in the composite rays, forming the entire structure in rays only one or two elements high. This relation obtains in all the higher Coniferae in the first instance ; but in *Larix*, *Picea*, and *Pinus*, where there is a notable increase in numbers, they also become interspersed with the parenchyma cells and eventually predominate over them, a feature which is especially characteristic of the hard pines. Efforts have been made to show that in all such cases the two kinds of elements succeed one another in a definite order from above downward, or the reverse, but our studies have failed to show that this is capable of practical application to the purposes of classification or even of phylogeny (13, 491). The great fact of importance for our present purpose, however, and one which stands out with much prominence, is that the ray tracheids are not a structural feature of the more primitive Coniferales, but only of the higher types, such as *Picea* and *Pinus*. Furthermore the primitive position for these structures is in the one- or two-celled rays, or correspondingly in the margins of the composite rays.

In *Thuja* and *Cupressus* the tracheids appear to stand by themselves, and they exhibit no special relations to the parenchyma elements which would permit of inferences as to their possible origin. In the genus *Pinus*, on the other hand, where the relations are somewhat complex, evidence does appear of such a nature as to suggest their derivation. In *Pinus inops*, *P. Torreyana*, *P. pungens*, *P. clausa*, *P. tæda*, *P. palustris*, and *P. cubensis* we frequently find thick-walled parenchyma cells and characteristic ray tracheids conterminous with one another. This does not mean a simple association, since nearly all such cases, as typically presented by *P. palustris*, also show a graduated structure of such a nature as to confirm the belief that the one passes into the other by structural gradations. That such is the case cannot be doubted, and if further confirmation were needed, it is afforded by the precisely parallel relations to be met with in the formation of resin cells and resin canals. A further fact of much significance from the standpoint of development is that such

interchangeable relations are peculiar to the highest types of the genus *Pinus*. But we may ask, What is the function of these structures which make their appearance only in the higher *Coniferæ*? What is the proper significance of their appearance there, and do any other plants offer parallel examples?

In the so-called medullary rays of *Lepidodendron selaginoides* (81, 141) there are numerous reticulated or spiral elements which are undoubtedly of the nature of tracheids, and they may be held to represent the ancestral form of the ray tracheids in the *Coniferæ*, toward which they bear the same relation that exists between the spiral protoxylem element and the characteristic wood tracheid with bordered pits. From this it is apparent that the ray tracheid of *Pinus* or *Tsuga* represents a primitive structure which reappears in response to conditions of growth and structural alterations of such a nature as to demand the interposition of more simple, because more primitive, elements for the proper performance of necessary functional activities. These activities, in the case of *Lepidodendron*, are probably expressed in the radial distribution of water (81, 141), and we are no doubt correct in assuming similar activities to be carried on in the higher *Coniferæ*. In all those species which present the primitive structure of the thin-walled ray cells, both fossil and recent, there are no tracheids to be found. As a tendency to thickening of the wall arises, there is also developed a sporadic tendency to the development of ray tracheids, as in *Thuya* and *Cupressus*. It is also a noteworthy fact that simultaneously with a general thickening of all the cell walls throughout the ray, as in the genus *Tsuga*, ray tracheids become a constant and prominent structural feature. This relation exists in *Pseudotsuga*, *Larix*, *Picea*, and *Pinus*, and it is a remarkable fact that as the type of organization advances, and the structural modifications of the wall become more profound, the tracheids gain steadily in numbers and importance until they finally replace the parenchyma cells more or less completely. Such facts serve to direct attention to the idea that by such progressive alteration the ray cells gradually lose their normal functional powers with respect to the radial distribution of water,

and under such circumstances it is imperatively demanded that this deficiency should be met through some other structures. Under these circumstances two alternatives are possible: first, that the thick-walled and useless cells should return to their primitive condition in opposition to the general course of development, and once more resume their appropriate functions. Such structural reductions do in reality occur in these very cases, as shown in *Pinus tæda*, etc., but it is to be observed that they are of the nature of a growth which has been arrested at such an early stage as to be devoid of many of the normal structural features. Furthermore it would be difficult, if not impossible, to obtain evidence from other plants in support of a hypothesis of this nature. It is true that in the case of girdled pines the heartwood may resume an activity long since lost, and thus take upon itself once more the function of the sapwood, and also to some extent the function of the bark; but such renewed functional power does not in any way involve structural modifications of existing elements, and cases of this sort cannot be cited in support of the hypothesis. It is therefore fair to conclude that such structural reduction and restoration of functional activity are accompanied by a partial diversion of energy to the preponderant tracheids.

The second alternative permits us to consider that in the ordinary course of development the ray cells gradually lose their functional activity as a result of extreme structural modification, and that this loss of power cannot be restored, even though the wall may return to a primitive condition of structure through various phases of atrophy. In accordance with this idea the tracheid would be introduced as the most natural because the original medium for such activities as are centered in the ray, and it would therefore acquire additional importance both numerically and functionally in direct proportion to the loss of power experienced by the parenchyma cells. This appears to be a reasonable interpretation, and in the light of observed facts it would seem to be the correct one.

A structural feature of great importance in the ray tracheid appears in certain inequalities of the upper and lower walls, which



take the form of toothlike projections into the cavity (fig. 26). In what may be regarded as the most highly developed tracheids the teeth project across the cell cavity until they meet and coalesce, thereby forming a more or less definite reticulation, which gives to the tracheid a very characteristic appearance. As seen in tangential section, such reticulations often appear as narrow bands crossing the cavity from side to side, thus giving the cell a varying aspect. Such dentate and reticulated tracheids are absolutely confined to the second section of the genus *Pinus*, in which they constitute one of the most characteristic features to the extent of 68.3 per cent of the species. A more detailed analysis of this feature, as applied to the hard pines, is desirable. In *P. resinosa* and *P. Thunbergii* the tracheids are simply dentate. In six species, represented by *P. Murrayana*, the teeth extend into definite reticulations confined to the summer wood; but in six other species, represented by *P. Jeffreyi*, such reticulations are sparingly developed throughout the ray. In *P. tæda* a transitional form appears. Typically this species shows the tracheids to be sparingly reticulated, but occasionally they are strongly reticulated throughout. This brings to mind the further fact that in all species which are sparingly reticulated there is a marked tendency to strong reticulation in the summer wood. In the thirteen remaining species the tracheids are uniformly strongly reticulated throughout the extent of the ray, and this feature attains its highest expression in *P. palustris* and *P. cubensis*. It is therefore manifest that we have to deal here with a graduated development of such a nature that the simply dentate tracheid is the most rudimentary, while the strongly reticulated is of the most advanced type of structure.

The value of the ray tracheid for taxonomic purposes depends upon (1) its occurrence in certain genera, and (2) its structural peculiarities. In the great majority of cases the simple wall of the tracheid affords no basis of specific differentiation, but in the various forms of dentate and reticulated walls of the second section of *Pinus* it is of well-defined value in this respect. *Pinus resinosa*, *P. Thunbergii*, and *P. koraiensis* are all characterized

by the occurrence of simple teeth, which are sometimes sparingly developed. This feature is intimately associated with the occurrence of large, simple, and single pits on the lateral walls of the ray cells. From this group *P. densiflora* may be differentiated by the reticulations in the tracheids of the summer wood. Among the hard pines *P. tæda* is distinguished by ray tracheids, which are typically sparingly reticulated throughout, but on the other hand *P. palustris* and *P. cubensis*, which probably represent the highest types of the genus, are at once separated from all other species by reason of the extent to which reticulations are developed.

The relations which the tracheids bear to the parenchyma cells in the general composition of the ray also have an important bearing upon specific differentiations. In the genus *Tsuga* the tracheids are sometimes interspersed, affording the first instance of a relation which later becomes most prominent in the higher genera, and the same relation is also expressed in *Pseudotsuga* and *Larix*. In *Picea* there is a somewhat stronger tendency to an interspersal which is only expressed fully in *Pinus*. In the soft pines eleven out of thirteen species show, as in the previous genera, that the tracheids, as a rule, are rarely interspersed; *P. aristata* forming a partial exception, as shown in a sparing interspersal. *P. monophylla* and *P. monticola*, on the other hand, show a strong interspersal of the tracheids, and in this respect they approach the hard pines. In the latter group we again find the first four species characterized by a rare interspersal; but passing on to the more highly developed species, such types as *P. clausa*, *P. palustris*, and *P. glabra* show that the interspersed tracheids are not only numerous but also that they eventually become conspicuously predominant and often constitute the bulk of the ray structure. It is evident, then, that such features possess an obvious value for diagnostic purposes, particularly in the genus *Pinus*, where the variations are numerous, well defined, and applicable to particular species or groups of species.

As displayed in tangential section, the medullary ray exhibits two principal forms, each of which presents features of great taxonomic and phylogenetic value. The type of structure which

prevails, and which may be regarded as the fundamental form of the ray, is that of from one to many cells superimposed in a single series of varying height (fig. 27). Such one-seriate rays are characteristic features of all the investigated recent genera. In 30 per cent of the genera there is a sporadic tendency to a multiseriate form as expressed in the development of rays which are two-seriate in part. Such enlargement is not confined to any particular portion of the structure, and within the limits of the same section it may arise at the center or at either end. It is never found in *Abies*, *Picea*, or *Pinus*, but it is met with in *Pseudotsuga macrocarpa*, three species of *Cupressus*, two of *Juniperus*, one each of *Sequoia* and *Araucaria*, and two of *Larix* (figs. 27, 28). In *Libocedrus* such tendency is much more pronounced, and the rays may be described as two- to three-seriate in part.

FIG. 27. *SEQUOIA SEMPERVIRENS*. Tangential section of a medullary ray showing a typically one-seriate ray of broad form.  $\times 280$

This feature is of so sporadic a nature that existing species afford no satisfactory evidence as to its origin or significance, but reference to *Cordaites* tends to throw some light upon this somewhat obscure problem. In fourteen species of *Cordaites*, three of which are European (28, 606–609), it is seen that the rays present four variants ranging from the strictly one-seriate form to one- to two-, rarely three-seriate.

The distribution is in the following percentage proportions:

1-2, rarely 3-seriate	21.4 per cent	2-seriate in part	50.0 per cent
1-2, seriate	14.3 " "	1-seriate	14.3 " "



FIG. 28. *TAXUS BREVI-FOLIA*. Tangential view of a medullary ray showing its two-seriate character.  $\times 280$

From this it would appear that *Cordaites* as a whole approaches the primitive, multiseriate ray, such as may be found in the Cycads, much more nearly than any of the existing species under consideration, and from this point of view it becomes possible to arrange a sequence showing the relative development in the following terms: (1) *Cordaites*, (2) *Libocedrus*, (3) all other genera, as enumerated above. The evidence of fossil plants, however, shows that caution must be exercised in our estimate of what constitutes the primitive ray. The structure of *Stigmaria* shows a preponderance of one-seriate medullary rays (81, 224), and that such are primitive rays cannot well be doubted. In general, however, we are probably not far from correct in the assumption that the highest form of the ray is expressed in its one-seriate character. Deviations from this would then require to be interpreted as vestigial features, which indicate a relatively lower type of organization in direct proportion to the increase of a tendency toward a multiseriate form.

In the majority of species the side walls of the parenchyma cells are thick and traversed by small pits. In the genus *Pinus* the wall is commonly thin, and it closes the orifice of a very large pit on the wall of the adjacent wood tracheid. This is notably true of the soft pines, in which the side wall either projects as a convex membrane, or it is concave and curves into the cell cavity. Such a feature is of very little if any importance except in *P. reflexa*, where the thin side walls almost invariably project so as to give the cells a correspondingly inflated appearance (fig. 29). It is not only apparent in a tangential section, but is very conspicuous in the transverse section (fig. 18), where the inflated walls are seen to project into the

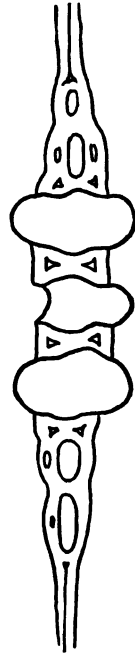


FIG. 29. *PINUS REFLEXA*. Tangential section of a medullary ray showing the typically inflated cells.  $\times 300$

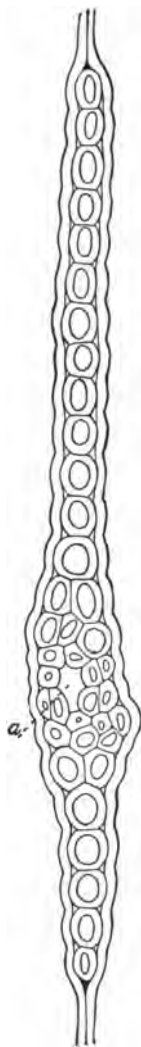


FIG. 30. *PSEUDOTSUGA DOUGLASII*. Tangential section of a fusiform ray showing (a) the typical resin canal with thick-walled epithelium, but devoid of thyloses.  $\times 280$

cavities of adjacent wood tracheids, thereby giving to the ray a beaded appearance. As an exceptional variation it possesses no apparent significance with respect to questions of descent.

The second form of the ray is that which has been designated as fusiform in reference to its characteristic outline (44, 39). Such rays occur in relatively few of the existing genera to the extent of 20 per cent. They occur typically in *Pseudotsuga*, *Larix*, *Picea*, and *Pinus*, and they are thus seen to be characteristic of the most advanced types. Among extinct species they are unknown except in the case of *Sequoia Burgessii* (46, 42-46) and *S. Penhallowii* of Jeffrey (25, 321), in which they present a remarkable exception to the general course of development and structure of that genus. The fusiform rays are peculiar in their structural features. They vary greatly in height as between different genera, and such variations also occur within a given genus, the extremes being met with in the genus *Pinus*, where *P. palustris* and *P. ponderosa* present the antithetic relations. In most cases they are much higher than the one-seriate rays with which they are associated, but this rule is subject to several exceptions. They are always distinguished by a broadening of the central tract by from two to several times the original dimensions, thereby becoming more or less multiseriate. These variations depend upon the nature of the included structure, which exhibits modifications directly related

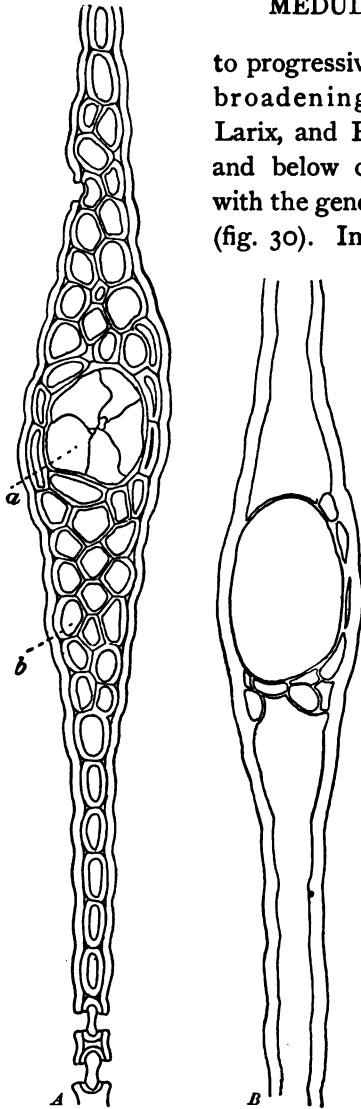


FIG. 31. *A. PINUS ALBICUALIS*. Tangential section of a fusiform ray showing a typical resin canal with (*a*) thyloses, and (*b*) rather thick-walled parenchyma.  $\times 280$ ; *B. PINUS PALUSTRIS*. Tangential section of a fusiform ray in part showing thin-walled parenchyma broken out.  $\times 280$

to progressive development of the genus. Such broadening arises abruptly in *Pseudotsuga*, *Larix*, and *Picea*, so that the terminals above and below consist of a single series of cells with the general structure of the one-seriate ray (fig. 30). In *Pinus* the broadening is less abrupt, diminishing in both direc-

tions somewhat gradually, thus giving rise to a region of lenticular form which occupies upwards of half the height of the ray, or in some cases constitutes the entire structure. From this it follows that in such types as *P. palustris* (fig. 31, *B*) the terminals, which are often prolonged to great length, may be linear and one-seriate, while in *P. ponderosa* the whole ray is lenticular in outline and the terminals consist of only one or two limiting tracheids (fig. 32). Within the region of the central tract the cells are all thick-walled in *Pseudotsuga*, *Larix*, and *Picea*, but in *Pinus* they are generally thin-walled, and in the hard pines this feature is emphasized by a degeneration of the tissue to such an extent that it is readily broken out in making sections, whence it characteristically appears either much broken up or entirely wanting. The principal feature of such rays, and the one which determines their form, is the

presence of a resin canal in each case. Such resin canals traverse

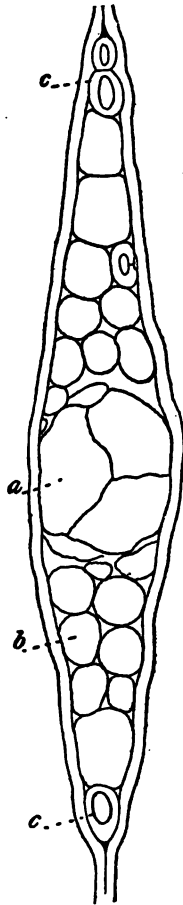


FIG. 32. *PINUS CLAUSA*. Fusiform ray showing (a) the resin canal with thyloses; (b) thin-walled parenchyma cells; (c) the terminals composed of only one or two tracheids.  $\times 280$

the ray continuously for its entire length. They present the same details of structure as the resin canals which lie within the xylem. In *Pseudotsuga*, *Larix*, and *Picea* the central canal is narrow, especially in the first two genera, and the epithelium consists of a single layer of thick-walled cells. In *Pseudotsuga* and *Larix* (fig. 30) thyloses are altogether wanting, but in *Picea* they are of sporadic occurrence. In *Pinus* (figs. 31 and 32), on the contrary, the canals are always distinguished by their great breadth; the epithelium is composed of from one to several rows of thin-walled cells, which are often resinous and often much disorganized, while thyloses are an invariable feature of the central canal.

A comparison of different genera and species shows that there is a somewhat striking variation in the number of one-seriate rays (tangential) to a given area of section. Such variations may arise within narrow limits in the same species, according to location and conditions of growth, but apart from this there are somewhat constant variations between different species, which may be expressed by the use of the relative terms "few" and "many." No attempt has been made to define such variations more exactly, but it is quite possible that a determination of the average number to a square centimeter or other

convenient unit might disclose a somewhat greater differential value than is at present apparent. A simple illustration will

serve to afford an idea of the rather limited specific value of this character. In *Taxus cuspidata* the rays are numerous, while in the two remaining species they are relatively few. The same feature applies to the differentiation of *Torreya nucifera* from the other species of that genus. In *Pinus clausa*, *P. serotina*, *P. Murrayana*, etc., the same rule applies, but in all such cases it cannot be accepted as final.

The height of the ray is subject to such variations, even within the same species, that it cannot be defined with sufficient accuracy to admit of its application to classification in more than a very general sense. It is true that the rays of *Gingko* are always low, while those of *Taxus* and *Torreya* are often high. In *Juniperus* they are commonly low, while in *Pinus* they range from low to very high. Such variations do not possess sufficient constancy to admit of either generic or specific application in the strict sense, though they not infrequently serve a useful purpose as controlling factors, and they are therefore incorporated in all the diagnoses. Variations in breadth have a much more definite value, since the element of constancy is well defined. The genus *Thuya* (fig. 33) may almost invariably be differentiated by this feature. In *Cupressus*, *C. thyoides* may be distinguished by a similar feature, while *C. arizonica* and *C. Goveniana* are equally well indicated by their great breadth. The same rule applies also to *Juniperus*, *Sequoia* (fig. 27), *Pinus*, and other genera, whence it appears that this feature is of specific value. It is always associated with and dependent upon the form of the component cells (tangential), which affords a means of distinguishing genera and species with much directness. The narrowly oblong cells of *Thuya* (fig. 33) serve to separate



FIG. 33. *THUYA GIGANTEA*. Tangential section of a ray showing the typically narrow and oblong cells.  $\times 280$



this genus without difficulty, since a similar feature occurs but rarely elsewhere, and then in such association as to make the differentiation clear. In *Juniperus* the genus is separable into four well-marked divisions: (1) round to oval or transversely oval, (2) rays broad, the cells oval to round, chiefly round; (3) chiefly oval; (4) rays narrow, the cells oblong to oval, chiefly oblong. The broadly oval and thin-walled cells of *Sequoia* separate it from associated genera. In *Picea* the genus may be subdivided according as the cells are (1) variable, round, oval, or oblong; (2) equal and uniform, oblong or oval.<sup>1</sup> *Cupressus* is similarly separable into groups. But it is not difficult to separate *C. arizonica* and *C. Goveniana* more specifically, by reason of their broad rays and very conspicuously transversely oval cells, from *C. pisifera* with its round or oval cells and *C. thyoides* with its narrow, oblong, rarely oval cells. In the genus *Pinus* attention is at once directed to *P. Murrayana* by the conspicuously round or transversely oval, very unequal, and variable cells.

The interspersal of the tracheids often imparts a characteristic appearance to the tangential aspect of the ray, especially in the genus *Pinus*, and more particularly among the hard pines. In this group the tracheids present very variable forms and sizes. In such types as *P. glabra* they are small, oval, or round, and wherever they occur they give rise to a marked local contraction. In *P. palustris* and *P. cubensis* they are commonly oblong and not infrequently they become several times higher than broad. As they are almost invariably narrower than the associated parenchyma cells, they cause a local contraction which sometimes extends over considerable distances. In *P. palustris* the predominance of the tracheids is carried so far that the rays are chiefly composed of them, and it then becomes appropriate to apply the term "interspersed" to the few parenchyma cells. In all of the more highly organized rays of the hard pines the appearance of the structure is so complex and variable that a proper

<sup>1</sup> The term "equal" here applies to cells of the same ray which are of the same width, "uniform" to the cells of all rays which are pretty constantly of one form, the contrasting terms being "unequal" and "variable" respectively.

diagnosis can be drawn only when we take cognizance of the principal aspects presented, and these are sometimes as many as four in number.

A consideration of the various structural features thus discussed in their relations to classification will show that no other portion of the stem possesses so many elements of importance as the medullary ray, which, in consequence, attains the highest value in this respect and affords differential characters of wide range, great prominence, and easy recognition, and is of primary importance in the differentiation of groups, genera, and species; and, as a general summary, the utility of these characters for such purposes is approximately indicated in the following tabulation:

1. Rays (tangential) of two kinds.	}	Generic.
2. Ray tracheids.		
3. Pits on the lateral walls of the ray cells simple or bordered.		
4. Terminal walls of the ray cells thin and entire or locally thickened.		
5. Form and character of the ray cell (tangential).	}	Specific.
6. Form and size of pits on the lateral walls of the ray cells.		
7. Ray tracheids dentate or reticulated.		
8. Direction and form of orifice of pits on the lateral walls of ray cells.		
9. Upper and lower walls of ray cells.	}	
10. Ray tracheids interspersed or marginal.		
11. Disposition of pits (radial).		
12. The number of pits per tracheid.		

The marginal cells of the ray — that is, those which terminate the ray above and below, as seen either in a radial or a tangential section — are usually somewhat different from those which constitute the bulk of the structure. This difference is expressed in a tangential section by their greater height and relatively narrower form. In a radial section it is expressed by the greater height, the somewhat thinner walls, and the sinuous form of the latter as they conform to the terminations of adjacent tracheids. In such deviations from the usual characteristics of the ray cells it is probable that those of the margin may be held to exhibit a tendency to the formation of ray tracheids of which they would

therefore be regarded as potential forms. This view gains strength from the fact that the ray tracheids first appear in just those situations; that when they are sporadic, as in *Abies balsamea*, they are interspersed and conterminous with the marginal cells; that their external forms and general aspect are the same; and that when the tracheids are fully developed and become constant features of the ray it is at the expense of the ordinary marginal cells, which then disappear. Furthermore Jeffrey has shown that in *Sequoia Penhallowii* (25), where the marginal cells assume a very characteristic form, they are also interspersed in the higher rays precisely as tracheids are in the rays of the higher Coniferæ. Another feature of these cells — to which Jeffrey has directed attention in *Sequoia Penhallowii* — is the presence of numerous crystals. This is unique among the Sequoias, and it is unknown in any other genus of the Coniferales except *Abies*, where, as Jeffrey also shows, a similar deposit of crystals is to be met with in *A. concolor*, *A. grandis*, *A. bracteata*, *A. nobilis*, and *A. magnifica*; but it is a feature of much more sporadic occurrence, since large areas of these species show no crystals, while in *Sequoia Penhallowii* they are exceedingly abundant. Jeffrey correctly regards this as indicating a certain relationship between these two genera (25), a connection, however, which is also indicated by other structural features, as pointed out by Penhallow some years since (44, 45).

## CHAPTER VII

### MEDULLARY RAYS (*continued*)

#### RELATIONS TO DEVELOPMENT

We are now in a position to determine the relations in which the various structural features of the medullary ray stand to development, and for this purpose it may be most convenient to discuss them in that sequence which is apparently consonant with the general order of evolution of the entire group.

It has been ascertained that bordered pits are characteristic features of the lateral walls of the ray cell in 72.4 per cent of the investigated species, and that in the remaining 27.6 per cent, among the higher types, simple pits predominate, but a closer scrutiny of this latter group discloses some features of more than passing interest. Reference to the table of anatomical data (Appendix A) will show that the change from bordered to simple pits is entirely confined to the genus *Pinus*, and that it does not arise abruptly as if in response to some unusual condition whereby a profound alteration in the usual course of development was induced; but it is effected by stages, showing that whatever influences were brought to bear, they operated gradually through a somewhat prolonged period of development, while here and there strong tendencies to reversion were manifested, and that the alteration was finally effected in a permanent way, only in the most highly developed pines. Commencing with *P. Lambertiana*, it will be observed that some species of the soft pines are characterized by simple pits. Among the hard pines *P. clausa* and *P. rigida* have bordered pits, while the six following species again show simple pits. We next come to a group of four species, with one exception (*P. Murrayana*) Japanese, in which there is a mingling of both bordered and simple pits, showing a decided persistency

of the primitive character in the face of conditions which involve a change. Following these are two species with simple pits, one with transitional features, five with simple pits, one with bordered pits, one with the transitional form, and the remaining six species with simple pits only. It will therefore be seen that these changes occur in waves, and that within the limits of forty-one species there are three complete and six incomplete recurrent phases. If we were arguing from purely theoretical grounds, all of these species should be arranged in such order as to show (1) bordered pits, (2) transitional forms, and (3) wholly simple pits, and we should thereby gain a perfect developmental sequence. But such a position would not be justified by other evidence of an equally if not more weighty character, and it is our object to interpret the facts as they are found. It has already been shown that the occurrence of simple pits in the pines is consonant with a higher type of development, and that the change is not only accompanied by sporadic reversions or survivals, as one may choose to regard them, but that the change as a whole is a process of reduction. From this point of view, then, we must regard the occurrence of bordered pits in *P. clausa*, *P. rigida*, and *P. pungens* as pure survivals of a more primitive structure, — a feature which is less perfectly expressed in such transitional forms as *P. koraiensis* or *P. inops*. But a mere mingling of the two kinds of pits in the same species is not the only evidence in this direction. The mingling of simple and bordered pits does not occur indiscriminately, but in accordance with a well-defined law to the effect that the former are characteristic of the spring wood throughout its entire extent, while the latter occur, if at all, only in the summer wood, where they might be expected, since the arrested development which might be complete in the case of relatively thin-walled cells could be readily overcome in part in walls of greater secondary growth. This in no way conflicts with the observed fact that in the majority of cases the usual course of development is such that the bordered pits of the spring wood very commonly become reduced to simple pits in the summer wood, in accordance with De Bary's law, as already stated in

application to other cases. Constancy in the structure of such pits has been found to be characteristic of *Cordaites*, *Gingko*, the *Taxaceæ*, and all the lower forms of the *Coniferaæ*, from which we may conclude that the bordered pit is essentially a primitive character. On the other hand, variation is a well-marked feature of the pit in the genus *Pinus*, as first expressed in the large oval or squarish and open pits of *P. resinosa* or *P. Thunbergii*, and as later appears with greater frequency in the smaller and very inconstant pits of *P. tæda* or *P. palustris*. Such variations, then, involving a gradual and complete transformation to the condition of simple pits, are characteristic only of the more highly developed pines, from which it may be concluded that it is a feature consistent with a relatively high order of development in exact accord with the principles governing parallel changes in the pits of the wood tracheids. They are also in harmony with the well-known principle that variation is always of a more simplified form in primitive types, but that it tends to greater diversification with advance in organization and general development, as a necessary sequence to the adjustment of the organism to a wider and more complex environment. Finally, it has been shown that the elimination of the bordered pit proceeds concurrently with the more complete organization of the ray tracheids, in response to a substitution of functional activities between these structures and the degenerate parenchyma cells. We may therefore conclude that extreme variation in the character of the pit is an expression of a higher type of development, and that from this standpoint such structures have a definite value in solving questions of descent.

The terminal walls of the ray cells present three variants with respect to secondary growth. All the more primitive *Cordaitales* and *Coniferales* are characterized by thin walls. *Cupressus* and *Juniperus* are chiefly distinguished by their thin walls, which are also locally thickened, a feature which has been shown to be due to incipient secondary growth. But such alterations are already foreshadowed in *Libocedrus*, where the local thickening of the wall is of a sporadic nature. In *Abies magnifica* and *A. grandis* there is a partial recurrence of thin and locally thickened

walls, which is pretty fully expressed in *A. concolor*. A similar recurrence is met with in *Pseudotsuga macrocarpa*, in *Picea polita*, and in *Pinus Parryana*, and it is also complete in thirteen of the most highly developed species of *Pinus*, where the walls have suffered extreme degeneration. Within the limits of *Picea* (1) and the soft pines (5) there are six instances in all of sporadic and partial survival of the thin and locally thickened wall. The first tendency to thick and strongly pitted walls is manifested in five species of *Juniperus*, and such development is fully expressed in what may be regarded as the three most highly developed species. Thick walls are then fully characteristic of *Abies*, — with a partial reversion in *A. concolor*, — of *Tsuga*, *Pseudotsuga Douglasii*, and *Picea*, with the exception of *P. polita*, five species of soft pines, and three species of hard pines. In *P. tæda* and *P. palustris* the walls are so degenerate that their structure cannot be satisfactorily determined, but they are presumably thin-walled.

From these facts it is manifest that the progressive thickening of the terminal walls accords with the general course of development, and once more making use of the principles already applied to the pits on the lateral walls, we are brought to the natural conclusion that (1) an increase in the thickness of the walls is evidence of a higher type of organization, and (2) that the sporadic recurrence of thin walls with local thickenings represents the persistence of a primitive character.

Ray tracheids probably constitute one of the most valuable of the structural elements as an indication of development. This has its foundation (1) in the fact, previously shown, that they arise as secondary structures from the parenchyma elements, with which they exhibit interchangeable relations, in direct response to the requirements of a higher degree of organization, and (2) in their general relation to progressive development. The complete absence of ray tracheids from the Cordaitales and Gingkoales, as also from the Taxaceæ and more primitive Coniferæ, while they are invariable features of the higher Coniferæ,

in which they attain their most complete development, admits of only one interpretation. The fact that they are exclusively features of the Coniferæ emphasizes their inferior value for determining the derivation of that group, while it points to their superior importance as a factor in the sequence of the various coniferous genera. They occur sporadically in *Thuya* (1), *Cupressus* (2), *Juniperus* (1), and *Abies* (1). They are prominent features of *Tsuga*, *Pseudotsuga*, *Larix*, *Picea*, and *Pinus*. Their invariable absence from *Sequoia* would appear to suggest that this genus is more primitive than *Thuya*, but there are other reasons which serve to suggest the opposite relation. Apart from this exception, it will be seen that in accordance with the relations exhibited in the table of anatomical data (Appendix A) the genera enumerated form a continuous series, commencing with those showing sporadic tracheids and ending with those in which such structures attain their highest expression. From this we are justified in the conclusion that the rare occurrence of tracheids in *Thuya*, etc., is to be interpreted as the first evidence of a tendency in development which is only fully realized at a later period, and this appears to be justified by a closer examination of the last five genera in this respect, since it is found that in them the tracheids not only show a progressive numerical development but their structure likewise becomes more complicated in direct relation to the evolution of higher types of genera and species. We must therefore look upon the tracheids with their thin, simple walls as the primitive form, while those with the strongest reticulations are of the highest type, the two being united by a transitional form characterized by the presence of simple teeth. The evidence at hand does not appear to justify the idea that the various genera have been segregated into small groups representing side lines of development, but it rather favors the thought that each genus is in itself a complete short line of descent, and that among these a prominent parallelism has arisen in the tendency toward the development of tracheids, — a tendency which has been carried to completion in the case of only five of the series, and in such



a way that in only a portion of one of these has that completion reached its highest expression.

The occurrence of two kinds of parenchyma ray cells is an exclusive feature of the genus *Pinus*, and its value for phylogenetic purposes is strictly confined to the relations of the various species of pines. The first appearance of this differentiation is among the soft pines in *P. aristata* and *P. edulis*. It is to be observed, however, that the thick-walled cells are always dominant, the thin-walled cells being interspersed among and continuous with them. No further evidence of such structural alterations is to be noted until we reach the more highly developed representatives of the hard pines. Among these definite transition forms occur in *P. Murrayana*, *P. Coulteri*, *P. Jeffreyi*, *P. virginiana*, *P. insignis*, and *P. cubensis*, while in *P. arizonica*, *P. ponderosa*, *P. Sabiniana*, *P. pungens*, etc., the original relations are exactly reversed and the thick-walled cells show a diminishing frequency until in *P. glabra* and *P. tæda* they are rarely met with. Such facts give effective proof of the belief that structural alterations of this nature are not only evidences of the highest type of development among the pines but also among the Coniferales as a whole.

The invariable absence of the fusiform rays from all except the four genera which attain the highest structural development, and their constant occurrence in all the species of such genera, presents an argument of great force as showing their relation to the evolution of advanced types. There is here no evidence of sporadic development, foreshadowing the general course of evolution, but the fusiform rays with their resin canals appear abruptly and permanently. Among fossil plants—except the genus *Pityoxylon*, which, being essentially *Pinus*, falls under the general rule—there is no instance of such structures outside of the four genera named, save in the case of the remarkable *Sequoia Burgessii*, from the Lignite Tertiary (51, 42), and *S. Penhallowii* of Jeffrey (25). As it will be necessary to further discuss the essential structure of the fusiform ray, we need not deal with it more in detail at the present moment.

## CHAPTER VIII

### WOOD PARENCHYMA

In our present studies we recognize as *wood parenchyma* all those elements which, in association with tracheids, have their major axes extended parallel with the principal axis of growth; and which, in accordance with accepted limitations, are characterized by their more or less cylindrical form, abrupt terminations, and relatively thin walls. Such elements do not occur in wood of the Cordaitales, and they are infrequent in the Ginkgoales, but they are somewhat conspicuous features of the Coniferales, where they acquire great prominence either because of their peculiar contents or their association with somewhat highly specialized tissues. They differ in their structure as in their special functions, though in the main they are connected with the production of resinous matter; and inasmuch as their most prominent feature is usually found in associated products of cellular activity, it will be most convenient to discuss them under specific names, which may serve to direct attention to their particular purposes in the plant economy. They may therefore be classified as follows:

Wood parenchyma:

- a. Crystallogenous idioblasts.
- b. Resin cells.

#### CRYSTALLOGENOUS IDIOBLASTS

The investigations of Eichler (15, 35) show that in Ginkgo the wood is characterized by the presence of wood-parenchyma cells, which take the form of short idioblasts of lenticular form in longitudinal section, and are distinguished by the storage of crystals of calcium oxalate. Such structures are peculiar to this

genus, in which they form a specific character of definite value, and it is therefore of importance that they should be described somewhat in detail.

In a transverse section (plate 18) the idioblasts, recognizable by their conspicuous crystals, may be seen scattered through the entire section without special reference to either the spring or the summer wood. Under a high degree of amplification it will be seen that they are often single, but quite frequently they

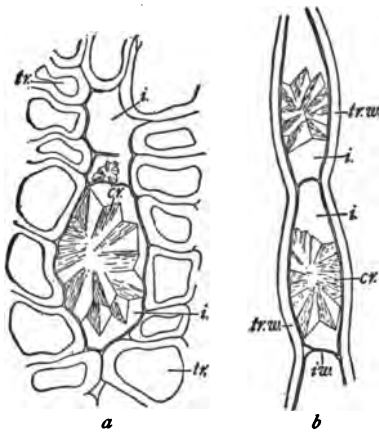


FIG. 34. GINGKO BILOBA. *a*, transverse section showing the occurrence and form of a crystallogenous idioblast; *b*, tangential section of the same. *tr.*, tracheids; *tr.w.*, tracheid walls; *i.*, idioblast; *iw.*, idioblast wall; *cr.*, crystals.  $\times 233$

are grouped in radial series of two or three, in which case one is generally much larger than the others (fig. 34, *a*). The form is narrowed tangentially and extended radially so as to be approximately lenticular, and the cavity is usually pretty well filled with a compound crystalline mass. The idioblast is situated in the line of one of the radial rows of tracheids, the continuity of which it interrupts. It is usually much larger than the individual wood tracheid, from which it also differs in the character of the cell wall, which is very thin and not infrequently

shows a want of continuity suggestive of obliteration in the course of development. In a radial section the idioblasts are usually of an isodiametric form, more rarely elongated longitudinally, and the compound crystalline mass somewhat more than half fills the cavity. In this section the walls are seen much better than in any other, and the relations of the idioblasts to one another are well exhibited. In a tangential section (fig. 34, *b*) the wall is also well displayed. The individual idioblasts are lenticular in form and the crystalline mass completely fills the cavity transversely,

but only about half fills it longitudinally. This section is the most useful for displaying the relations of the idioblasts to the adjacent tracheids, inasmuch as the limits of the walls of the latter are much more clearly defined. As seen in the tangential section, the idioblasts fall into a single longitudinal series, which may not embrace more than two or three members, but more commonly there are upwards of twenty-one in a series. Not infrequently the chain of crystals will be found to be interrupted for some little distance, but the continuity of the idioblasts will then be seen to be uninterrupted through the development of cylindrical elements of uniform but smaller diameter and devoid of crystals, from which it would appear that the lenticular or rounded form, as determined by the particular plane of section, is not the normal form of the cell, but that such special form results from the growth of the crystal, which must have been deposited when the tissue was in a formative stage of development. This is made apparent in another very striking manner. In any tangential exposure of such a series it may be seen that the terminal member does not necessarily occupy all the space between the walls of adjacent tracheids. There is thus developed an intercellular space of variable dimensions, which may be quite small or may be so extensive as to suggest that the crystals were formed in such spaces and not in closed cells. Such spaces are obviously not the result of that splitting which is ordinarily incident to the growth of tissues, but they clearly arise as a secondary effect incident to the development of the crystalline mass and the pressure of this latter upon the surrounding parts.

#### RESIN CELLS

In a large proportion of the Coniferales the wood is characterized by the presence of more or less numerous wood-parenchyma cells. These are always distinguished by their cylindrical form and transverse terminations. They are invariably associated with the production of resin, either as entering into the composition of resin passages or as isolated cells. It is this latter

group with which we are most particularly concerned at the present moment, and as, with very few exceptions, they are uniformly characterized by the presence of resin, which gives them a distinctive appearance, I prefer to describe them as *resin cells* rather than by the more commonly employed designation of *wood parenchyma*, which conveys no suggestion of their special function and most prominent feature.

The resin cells are found to be entirely wanting in those species of *Taxus* (4) and *Torreya* (3) which are included in the present studies. They do occur, however, in *Podocarpus*, where they present the usual structural features, but they are there remarkable for their number and the great abundance of massive resin which they contain. This distribution in the *Taxaceæ* does not altogether accord with the conclusions of Eichler (15, 35), who states that they occur very sparingly in the *Taxaceæ*, but makes no mention whatever of their presence in *Podocarpus*, where they are much too prominent to escape even the most casual observation.

In the *Coniferæ* resin cells are characteristic of all genera except *Picea* and *Pinus*, where they are replaced by resin passages, of which they form essential parts. They are, therefore, features in the wood structure of twelve genera, and they are constant characteristics of all their species, with very few exceptions. Such exceptions apply exclusively to the genus *Abies*, in which four species — *A. Fraseri*, *A. lasiocarpa*, *A. Veitchii*, and *A. balsamea* — are wholly devoid of such structures.

The recognition of the resin cells presents no difficulty in the great majority of cases, because of the abundance and depth of color of the resinous contents. This finds its most complete expression in *Taxodium*, *Sequoia*, *Cupressus*, etc. In *Abies*, on the other hand, where these cells have experienced extreme numerical reduction, and where there also seems to be a corresponding reduction in their secretory power, it is impossible to recognize them in this way. In such cases it is often possible to distinguish them by their slightly different form and somewhat thinner walls as compared with the adjacent wood

tracheids, by their situation slightly in advance of the outermost row of summer wood tracheids, and most particularly by their pitted terminal walls when the latter lie near the plane of section. This last feature may also be relied upon in all other cases when any element of doubt is involved (fig. 35). In longitudinal section the characteristic form of the cell serves to distinguish it beyond all doubt, even in the absence of resinous contents. Whether exposed in radial or tangential section the cell has the form of a narrow cylinder upwards of  $300\ \mu$  in length, and always several times longer than broad, except in cases where

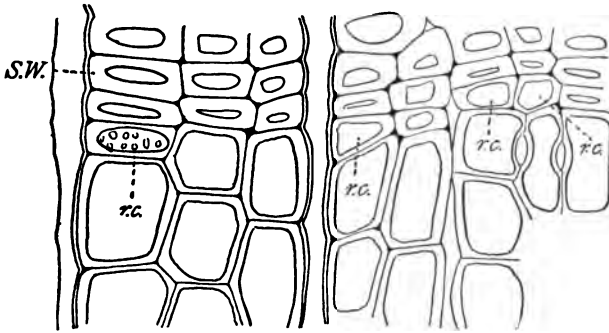


FIG. 35. *ABIES AMABILIS*. Transverse section showing the position and structure of the resin cells (*r.c.*) on the outer face of the summer wood.  $\times 300$

there is a definite tendency, through aggregation, to the formation of resin canals.

The resin cells sometimes occur in pairs, but more generally as isolated structures separated by one or more tracheids. The terminal walls are transverse and more or less strongly marked with simple pits. The side walls, especially the radial, are provided with simple pits, though often few in number, and this feature serves to a large extent to assist in their differentiation from adjacent tracheids of similar form (fig. 36, *c*). It nevertheless not infrequently happens that in transitional forms, such as are met with in *Sequoia sempervirens* (fig. 36, *c*), bordered pits occur on the lateral walls.

The resin is in all cases massive and often very abundant. In such genera as *Taxodium* (plate 30) or *Sequoia* (plate 36) it

completely fills the entire cell cavity, but in *Larix*, *Tsuga*, and *Pseudotsuga* it takes the form of a peripheral layer in immediate contact with the inner face of the cell wall (plate 44). The reduction thus indicated is, in some species, carried to such an extent that the resin is barely recognizable, while in *Abies* it is wholly wanting.

A relation of more than ordinary interest is that of the resin

cells to certain forms of tracheids. In *Sequoia sempervirens* it commonly happens that the resin cells lie in immediate contact with tracheids of special form. These structures are wholly unlike the wood tracheids among which they are found, but they are, in all essential respects, like the tracheids of the medullary rays. They have the form of long, cylindrical elements with abrupt terminations, and they thus bear an external re-

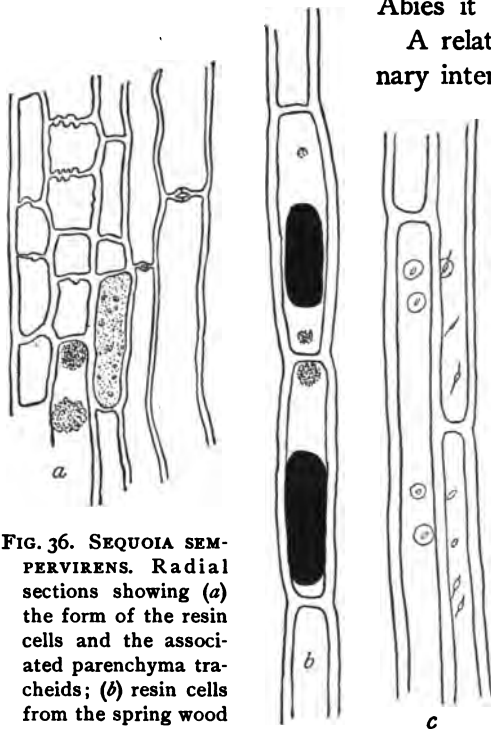


FIG. 36. *SEQUOIA SEMPERVIRENS*. Radial sections showing (a) the form of the resin cells and the associated parenchyma tracheids; (b) resin cells from the spring wood showing the form of the resin; (c) resin cells showing transitional forms with bordered pits.  $\times 200$

semblance in form to the wood-parenchyma cells with which they are associated. They differ, however, in the distinguishing presence of bordered pits upon their side and terminal walls (fig. 37, a). The relation of these two elements is nevertheless a much more intimate one than is implied by mere association. In *Sequoia* an interchangeable relation is manifested, as already pointed out, in the occurrence of resin cells with bordered pits

(fig. 36), while in *Abies amabilis* (fig. 37) resin cells and tracheids also form a conterminous series. It is thus obvious that we have here precisely the same interchangeable relations that have been found to occur in the medullary rays, and it is evident the one element must arise through modification of the other. The precise order of this sequence is not altogether clear from the available data, but the fact that ray tracheids are derived from their associated parenchyma cells, and that in such types as *Podocarpus*, *Taxodium*, etc., the resin cells occur without tracheids, while the latter do occur in *Sequoia* and especially in *Abies*, seems to justify the inference that here also they are derived forms, having their origin substantially in special modifications of the parenchyma elements. In view of these relations it is necessary to distinguish such elements as *parenchyma tracheids* in order to establish their proper identity and differentiate them from the wood tracheids which have a wholly different origin, as well as from the ray tracheids which have a wholly different location. It is probable that the parenchyma tracheids also serve a similar purpose to the ray tracheids with respect to the distribution of nutrient fluids. The origin of the parenchyma tracheids as suggested finds support in the statement of Eichler (15) that the wood parenchyma arises through the activity of the cambium cells, abundantly in the Cupressineæ and Abietineæ, forming in exceptional cases the epithelium of the resin canals, since it at the same time shows how the parenchyma tracheids arise, and how they may be intimately connected with the wood parenchyma; but it finds additional support in a knowledge of the genesis and structure of the resin passage.

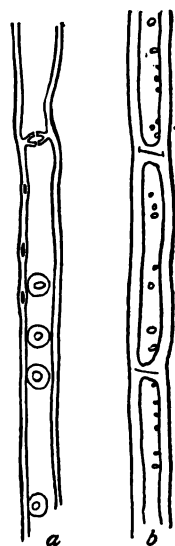


FIG. 37. *ABIES AMABILIS*.  
Radial section showing  
(a) the structure of the  
parenchyma tracheids;  
(b) the structure of the  
resin cells; a and b being  
normally conterminous.  
× 200



In *Sequoia* and *Abies* we have two genera which are remarkable for their transitional forms of structure, affording a fairly clear conception of the genesis of the resin passage. In each case there is a well-defined tendency toward the aggregation of the resin cells into compact groups which take the form of longitudinal strands, inclosed on all sides by the accompanying parenchyma tracheids. Under such circumstances the individual cells undergo a continual reduction in length until they eventually become but two or three times longer than broad, or they may even become isodiametric. This change is not accompanied by any alteration in the thickness of the walls in the earlier stages of development, but as a result of such a shortening the effect is to bring about the concentration of a greater number of simple pits within a given area. Such cells, therefore, are always more strongly pitted than those which are isolated and of greater length. When aggregates of this sort have attained to a certain degree of development a line of cleavage arises in the center of the mass and results in the formation of an intercellular space which, according to Eichler (15), always arises schizogenously. This space is short and either isodiametric or but little longer than broad, the length coinciding with the principal axis of growth. Such cystlike reservoirs or sacs represent the primitive form of the resin canal, and they are typically developed in *Sequoia*, *Abies*, and *Tsuga*. They always form a continuous series extending in a direction parallel with the axis of growth; but as the type of organization advances, they merge, forming a continuous canal such as may be found typically in *Pseudotsuga* or *Pinus*. From these statements, then, it is clear that the parenchymatous resin cells undergo modification in two directions, passing into parenchyma tracheids on the one hand, and on the other becoming shorter and shorter, according to conditions of aggregation, until they pass into short cells which eventually constitute the epithelium structure of the somewhat complicated resin passage, the latter thereby becoming the expression of a peculiar aggregation of resin cells. Whatever the stage of development may be, the resin passage is always

found to be composed of structural elements arranged in the following order from without toward the center : (1) parenchyma tracheids, (2) resin cells eventually forming an epithelium, and (3) the central reservoir in the form of a cyst or canal. This structure is fully exemplified in the genus *Pinus*, where the highest form of development is attained.

While the occurrence of resin cells in particular genera is a feature of great taxonomic value, their importance in this respect is greatly emphasized by the particular form of their distribution and the constant tendency they exhibit toward the formation of definite aggregates. In *Thujopsis* (plate 24) and *Cryptomeria* (plate 26) the resin cells are always scattered throughout the entire transverse section, and they show no tendency to the formation of aggregates. In *Podocarpus*, where there is a notable increase in numbers, the same general law of segregation prevails, but there is nevertheless a somewhat well-defined tendency toward aggregation. In *Thuja* 66.6 per cent of the species show definitely scattering cells, 33.3 per cent show the cells to be scattering with a tendency toward a more compact disposition, while in 33.3 per cent the cells fall into well-defined aggregates or an approximation to such an arrangement. The genus *Sequoia* is characterized chiefly by the widely scattering distribution of the resin cells (plate 36), but in *S. sempervirens* there are individual cases in which there is also a definite aggregation into groups. In *Cupressus* 53.9 per cent of the species are distinguished by the presence of widely scattering cells, which become definitely arranged in zones in 38.4 per cent, and aggregated into groups in 7.7 per cent of the species. It will be observed here that this feature of distribution is, on the whole, more pronounced in the relatively primitive genera, and that it diminishes in force in the genera of a relatively high order.

In *Taxodium* (plate 30) and *Libocedrus* (plate 32), both of which are distinguished by the presence of very prominent resin cells, these structures are disposed in well-defined zones which are concentric with the growth rings and lie either in the spring or summer wood, or in both. This is to be interpreted as a definite

tendency to aggregation, which is nevertheless not fully expressed, since in each case there are numbers of cells which are not zonal in their distribution, but which conform to the law applicable to *Thujopsis* and *Podocarpus*. In *Juniperus* the cells are typically zonate, being also scattering in only one species. In *Abies* only 63.6 per cent of the species bear resin cells. These are neither scattering nor zonate in the sense of the previous types, but it is to be observed that in 50 per cent of such cases, or in 36.3 per cent of all species, they are aggregated in groups as a preliminary step to the formation of resin passages. On the other hand, 36.3 per cent of all species show the resin cells to be few, inconspicuous, nonresinous, and scattered along the outer face of the summer wood. This, for reasons which will appear more fully later, is to be regarded as a phase in distribution leading to the final obliteration of such structures, which is fully accomplished in 36.4 per cent of all the species as represented by *A. balsamea*, *A. Fraseri*, *A. lasiocarpa*, *A. Veitchii*. This last form of distribution is wholly typical of *Tsuga* (plate 44), in which there are no other resin cells than those on the outer face of the summer wood. Finally, in *Picea* and *Pinus* there are no separate resin cells in any of the situations described, since they have been completely replaced by highly organized resin passages. It thus appears that the distribution of the resin cells presents four variants which bear a direct relation to the organization of resin passages, as the latter eventually replace the former. These facts will appear somewhat more clearly from the summary in the table on opposite page.

From such data it is clear that the distribution of the resin cells bears an important relation to the recognition of subgeneric groups and even of species. But viewing these structures from the broader standpoint of the Coniferales as a whole, it is obvious that they must be placed among the structural elements which belong to the first rank for taxonomic purposes.

We are now in a position to determine what relation, if any, such resin-bearing elements bear to questions of phylogeny, and we may first of all consider the resinous tracheids. These

## PERCENTAGE DISTRIBUTION OF RESIN CELLS

	NUMBER OF SPECIES	PER CENT OF OCCURRENCE	SCATTER- ING	IN ZONES	GROUPED	ON THE OUTER FACE OF SUM- MER WOOD
Gingko . .	1	000.00				
Dammara . .	1	000.00				
Araucaria . .	3	000.00				
Torreya . .	3	000.00				
Taxus . .	4	000.00				
Thujopsis . .	1	100.00	100.00			
Cryptomeria	1	100.00	100.00			
Podocarpus .	1	100.00	100.00	(100.00)		
Thuya . .	2		66.600			
	1 = 3	100.00		33.30		
	1		(33.30)			
Sequoia . .	2 = 2	100.00	100.00			
	1				50.00	
Cupressus . .	7		53.90			
	5 = 9	100.00		38.40		
	1				7.70	
Taxodium . .	1	100.00	(100.00)	100.00		
Libocedrus .	1	100.00	(100.00)	100.00		
Juniperus . .	11 = 11	100.00		100.00		
	1		1.10			
Abies . . .	4 = 7	100.00				36.30
	5				45.50	
Tsuga . . .	2 = 5	100.00			33.30	
	5					100.00
Pseudotsuga	2	100.00				100.00
Larix . . .	4	100.00				100.00
Picea . . .	10	000.00				
Pinus . . .	41	000.00				

structures have been seen to be peculiar to Dammara, Araucaria, and Abies, in which they occur only in certain species. In answering this question we cannot avail ourselves of evidence derived from fossil plants, since it is, in such cases, of a negative character. Neither Cordaites nor Araucarioxylon affords definite proof of the presence or absence of such structures, since they do not appear in any of the published diagnoses, and our own studies have not resulted in their recognition. If originally present, they

must have been obliterated in the course of fossilization. We must therefore depend entirely upon such evidence as is afforded by existing species. From this point of view it is obvious that they furnish no evidence as to the origin of either of the three genera in which they occur. It is, on the other hand, possible to determine from other data that both *Dammara* and *Araucaria* are much inferior to *Abies* in point of structural organization and development, and from this we may be permitted to conclude that the resin tracheids of *Abies* are vestigial forms of elements which were typically developed in *Dammara* and *Araucaria*, and possibly characteristic also of their progenitors. If such inferences are to be regarded as justifiable, they go far to support the idea of a common origin for all three genera, and they thus lend force to conclusions which lead to the same result, but upon the basis of independent data.

From a study of the distribution of the resin cells it is apparent that they fall into four categories in which the typically segregated cells may be held to represent the most primitive form of disposition. This view is greatly strengthened by the observation that in all such cases the resin cells are rarely if at all accompanied by parenchyma tracheids, while the structure of the cell is farthest removed from that which is found to enter into the composition of resin passages, whence they are also to be regarded as of a primitive character. This view is supported by the observed fact that those genera and species in which such segregations occur are also of a relatively primitive type. With an advance in organization, there is a tendency to the formation of aggregates as expressed in the zonal distribution of *Taxodium*, *Libocedrus*, or *Sequoia*, where we also find the definite formation of groups of cells which later exhibit the initial stages in the formation of a definite canal. But in *Sequoia*, as also in *Abies* where similar changes take place, the more complete aggregation of the cells is invariably accompanied by structural alterations whereby they become greatly shortened and more strongly pitted, while they are always accompanied by parenchyma tracheids with which they are interchangeable. In this connection

it is also to be noted that the aggregates in *Sequoia*, *Abies*, and *Larix*, leading to the formation of resin sacs, are always disposed in a zonal manner, conformably to the zonal disposition of the separate elements, — a relation which is in direct harmony with the view already advanced, that the zonal disposition of the isolated cells is an advance upon the strictly segregated form, and that it leads directly to the formation of resin passages. Following upon the zonal distribution, a more complete aggregation results in the formation of local groups of short resin cells ultimately leading to the formation of a true resin canal. Such a feature of distribution, occurring in genera which, from other data, may be shown to be relatively high in development, is in itself significant; but we further find that the scattering, zonal, and grouped forms bear such relations to one another that the real succession is in the order already given. Thus while both species of *Sequoia* are characterized by scattering cells, *S. sempervirens* also shows them aggregated to form groups and eventually imperfectly organized resin canals; or, in *Cupressus*, the transition is expressed in a more complete form, involving all three modes of distribution. In *Tsuga* there is an obvious tendency toward the elimination of the resin cells, which are now greatly reduced in numbers and confined to the outer face of the summer wood. In *Abies* a similar tendency is also manifested, but it is expressed in a different way, and just here we must note a fact of more than ordinary significance. Resin cells are present on the outer face of the summer wood in *A. grandis*, *A. concolor*, *A. amabilis*, and *A. magnifica*. Groups of resin cells are present in *A. nobilis*, *A. concolor*, *A. bracteata*, and *A. firma*, but it will be seen that in only one case — *A. concolor* — are the two forms of distribution presented in the same species. This is in direct conformity with the idea that the resin passage eventually displaces the resin cell, bringing about an obliteration of the latter, and it goes far to support the idea that with respect to these particular structures the genus *Abies* occupies a transitional position, standing next to *Picea* and *Pinus*, from both of which the resin cells have completely disappeared.

Furthermore, from another point of view, the gradual replacement of the resin cells appears to be indicated by a corresponding reduction in the contained resin. Nowhere is the resin so abundant in the resin cells as in those genera like *Podocarpus* and *Taxodium*, which show no development of resin passages, even in their most simple forms; but with the development of resin sacs, as in *Abies* or *Sequoia*, or of resin passages, as in *Larix* and *Pseudotsuga*, there is a remarkable diminution of the resin, apparently in direct response to its more ready production by more specialized structures.

The genus *Abies*, then, appears to form a transition group, having parallelisms with *Dammara* and *Araucaria* through the occurrence of resin tracheids; with *Thuya*, *Cupressus*, etc., through the survival of isolated resin cells approaching obliteration; with *Tsuga*, *Larix*, and *Pseudotsuga* through the development of rudimentary resin canals leading to the formation of definite resin passages; and with *Sequoia* through the survival of isolated resin cells and the development of rudimentary resin canals. Through these parallelisms the connection appears to be most direct with *Sequoia*, on the one hand, and with *Tsuga*, on the other. This relation of *Sequoia* to *Abies* has been shown by Penhallow on former occasions (59), and has more recently been indicated in other ways by Jeffreys (24); but so far as the present evidence is of value it would not permit us to infer that *Sequoia*, *Abies*, and *Tsuga* form a continuous and conterminous series in the order given, but rather that they represent separate, though short, side lines of development, between which the general sequence is manifested.

## CHAPTER IX

### RESIN PASSAGES

#### STRUCTURAL

Our studies of the resin cell have shown how peculiar aggregates of these structures lead in a natural way to the organization of resin passages, the structure of which it is now necessary to discuss somewhat in detail, and in doing so it will be most profitable to have reference to (1) the primitive form, (2) the intermediate form, and (3) the advanced or fully organized form.

The primitive form of the resin passage is to be found in *Tsuga*, *Abies*, and *Sequoia*, and inasmuch as within these genera they exhibit differences in organization which correspond approximately to the sequence given, it will be necessary to discuss them somewhat in detail, with special reference, however, to *Sequoia*. This genus possesses special interest with respect to the occurrence and organization of secretory reservoirs, since it is in all probability not only the most ancient genus in which such structures occur, but it is, so far as I am aware, the only genus affording special data with respect to important variations of structure and mode of occurrence. Being also, on the whole, the most primitive of the three genera, it may be dealt with first.

In *Sequoia sempervirens* the secretory reservoirs occur in rows within the initial layers of the spring wood,<sup>1</sup> and they therefore lie exactly on the outer face of the summer wood of the previous year. Within this row the reservoirs are contiguous, and in many cases they become confluent so as to form a

<sup>1</sup> The apparent occurrence of these structures in the summer wood is due to the presence of two growth rings of very unequal degree of development, the outermost of which may have only one or two rows of tracheids in addition to the resin cysts.



more or less extended and continuous compound reservoir, lying tangentially. In their most rudimentary forms they present the aspect of simple aggregates of resin cells without any differentiation of a resin sac or of an epithelium. In a more advanced stage of development there is produced a central cavity in the form of an intercellular space (fig. 38, *C'*) which has obviously originated schizogenously. About this the resin cells are generally flattened radially and disposed in such a manner as to suggest the future development of a definite, limiting layer or

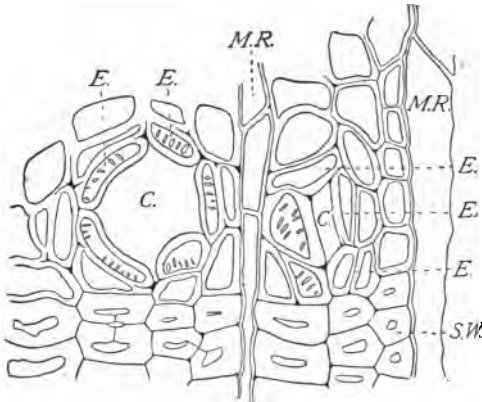


FIG. 38. *SEQUOIA SEMPERVIRENS*. Transverse section showing two contiguous resin cysts: *C*., completed and with a normal epithelium (*E*.); *C'*., an intercellular space as the rudiment of a cyst with imperfectly developed epithelium; *M.R.*, the medullary ray; *S.W.*, the summer wood.  $\times 225$

epithelium. In the completed form of the structure the central space has broadened out and taken a circular form, assuming the character of a definite cyst bounded by as definite a limiting epithelium in which the cells are always flattened radially and disposed concentrically (fig. 38, *C*.). Externally to these cells there may be a second layer of similar resin

cells, constituting the outer epithelium, while the whole is inclosed on three sides by a layer of parenchyma tracheids which are exceedingly like the associated tracheids of the spring wood, but from which they may usually be distinguished by (1) their greater size and relatively thinner walls, and (2) the occurrence of bordered pits on the tangential and terminal as well as upon the radial walls. Such parenchyma tracheids never occur in the adjacent summer wood for very obvious reasons, but on the radially opposite side of the reservoir they are very commonly flattened radially (fig. 39), and they not infrequently present the same

structural aspects as the epithelial cells. The interchangeable relation between resin cell and parenchyma tracheid as already shown would lead us to suspect a substitution in the composition of the epithelium, and such substitution does actually occur, since it is often to be noted that the second and third rows may be made up, at least in part, of tracheids.

In a longitudinal radial section the reservoir is found to have the form of a sac of varying form and size, but generally elongated

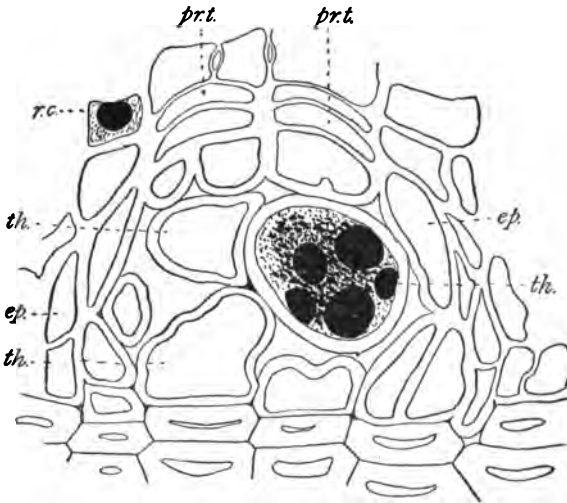


FIG. 39. *SEQUOIA SEMPERVIRENS*. Transverse section of a resin cyst showing an associate resin cell (*r.c.*); the epithelium (*ep.*); the thyloses (*th.*), one of which contains resin, and one of which is directly derived from an epithelium cell; the parenchyma (*pr.t.*).  $\times 300$

parallel with the axis of growth and completely closed at both ends (fig. 40). The epithelium, which immediately defines the limits of the sac, generally consists of short, cylindrical cells, while in the second or outer layer the cells become much elongated, being several times longer than broad. Beyond this, the third layer consists of parenchyma tracheids, readily distinguishable whenever the terminal walls lie near the plane of section, or otherwise recognizable, as already indicated. Certain deviations from this typical structure require examination. The resin sacs

are placed in vertical series of indeterminate extent, but at varying intervals of such a nature that they may sometimes be separated only by a rather thick wall of short resin cells. At other times they are somewhat distant and separated by an extensive vertical tract of resin cells. From this it is obvious that in any given

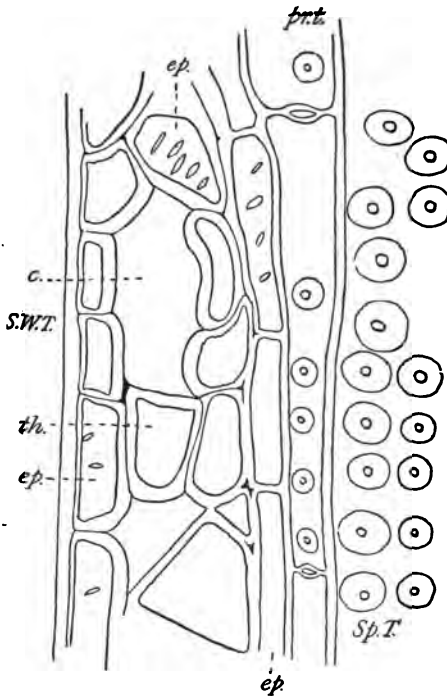


FIG. 40. *SEQUOIA SEMPERVIRENS*. Radial section of a resin cyst showing the epithelium (*ep.*); the central cyst (*c.*) with a thylosis (*th.*); parenchyma tracheids (*pr.t.*), and a tracheid of the spring wood (*Sp.T.*).  $\times 300$

plane of section there will be a great diversity of aspects presented, but in the main exhibiting structural gradations in the development of the reservoir, as already recounted. In some cases thick-walled cells of circular outline may be seen in transverse section to stand out from the general line of the epithelium and lie within the cavity proper. More rarely such cells are so multiplied as to fill the entire cavity, and they may themselves be filled with granular resin. Such features are clearly defined (fig. 39), and it is evident from the way in which such cells originate from the epithelial cells that they are of

the nature of thyloses. A longitudinal section through such a reservoir (fig. 41) shows how such thyloses occupy the entire cavity of the cyst, while in other cases they may be purely local (fig. 40). Among fossil *Sequoias* similar thyloses form a most characteristic feature in the resin passages of the medullary rays in *S. Burgessii* and *S. Penhallowii*.

In *Tsuga caroliniana* there are no secretory reservoirs, but just in the region between the spring and summer wood of the same growth ring there are peculiar aggregates of resin cells of a more or less rounded outline, forming a continuous series of considerable extent. An analysis of these aggregates shows them to be composed of thick-walled and rounded resin cells, among which there may be a small central, intercellular space without any definite organization of epithelium. In such aggregates the component cells are far less resinous than the isolated resin cells of the same section. The parenchyma tracheids are not clearly distinguishable from the associated wood tracheids. In radial section the cells are seen to be very variable, thick-walled, and sometimes with more or less prominent intercellular spaces. Between the rays they are several times longer than broad, but opposite the rays they are short, cylindrical, and more copiously pitted; while sometimes they may be seen to merge into ray elements and thus to continue their course at right angles to their primary direction. A careful comparison of these cell aggregates with those of *Sequoia* and *Abies* leaves little room for doubt as to their structural and functional identity, and we cannot do otherwise than conclude that they represent the most primitive structural condition which is capable of directly giving

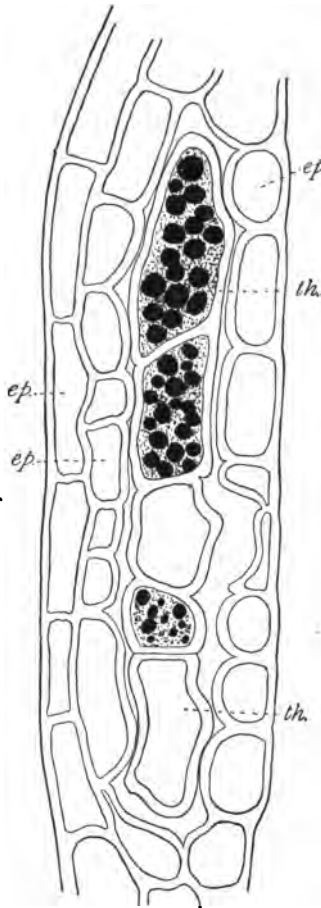


FIG. 41. *SEQUOIA SEMPERVIRENS*. Radial section of a resin cyst showing the epithelium (*ep.*) and the thyloses (*th.*), which completely fill the cyst, and several of which are resinous.  $\times 225$

rise to definite cysts by central cleavage, and that such cysts are precedent to the formation of canals.

In *Tsuga Mertensiana* the secretory reservoirs are disposed like those of *Sequoia*, on the outer face of the summer wood, where they form tangential series. They exhibit all the gradations from simple cell aggregates without a central space to perfectly formed cysts with a definite epithelium. This latter is in one, more rarely in two, rows, and it is composed of more or less rounded or radially flattened elements. The parenchyma tracheids are few in number, and they are not readily distinguishable from the adjacent wood tracheids. In longitudinal section the reservoirs are variously rounded or oblong cysts, contiguous or isolated and forming a longitudinal series. In their general form and structure they are essentially the same as in *Sequoia*.

In the genus *Abies* secretory reservoirs occur in at least four species, where they form more or less extensive tangential series, within which they are usually contiguous and more or less confluent. They present the same general variations in structural organization as in *Tsuga* and *Sequoia*, but in *A. concolor*, and less conspicuously in *A. nobilis*, they are often extended in a radial direction so as to become narrowly oval or oblong and several times longer than broad. The epithelium consists of a well-defined structure composed of from one to three rows of cells. The first row, immediately bordering upon the canal, consists of rounded or oval and thick-walled cells, which are much smaller than those of *Sequoia* and similar to those of *Tsuga*. They are always characterized by an abundance of strongly defined, simple pits, and many of them contain resin, which usually takes the form of rounded granules of diverse sizes. The parenchyma tracheids are so nearly like the accompanying wood tracheids as, in some cases, to be separable with some difficulty, but they generally surround the resin sac, at least within the limits of the spring wood, and they not infrequently replace the parenchyma cells of the epithelium more or less completely. Not infrequently they form somewhat extended radial series from the epithelium into the spring wood, as in *Picea* (fig. 43). In such cases they are

usually recognizable by their rather unusual size and thinner walls, and in addition they commonly show bordered pits on the tangential walls. When the terminal wall lies sufficiently near to the plane of section it shows from one to several rather large bordered pits, and by this feature such tracheids may be located with much certainty. Thyloses have been definitely noted only in the case of *A. concolor*, in which species they are essentially of the same general character as in *Sequoia*. They are thick-walled and either isolated or so numerous as to fill the entire cyst. In one case of contiguous cysts an epithelial cell was found to form thyloses in both cysts, — in the one case giving rise to an isolated cell, in the other forming a tissue which nearly filled the entire cavity.

In radial section the reservoirs are round or oblong cysts of variable size, and they are either contiguous or distant. In the former case they rarely or never become confluent, but they maintain their separate identity, as in *Sequoia* and *Tsuga*. In the latter case the intervening region is occupied by an aggregate of resin cells in all essential respects like those in the same regions of *Sequoia* and *Tsuga Mertensiana*, or like the aggregates which are generally characteristic of *Tsuga caroliniana*. The inner epithelium usually consists of short cylindrical and strongly pitted cells, which in the second and third rows become successively longer and less strongly pitted, so that those in the outer row may be identical in form and markings with the isolated resin cells. In the two outer rows the cells not infrequently show bordered pits on their radial walls, thus presenting transitional forms which gradually pass over into tracheids, and the one then replaces the other. The parenchyma tracheids, which are always most characteristic of the spring wood, are always distinguished by the presence of large and prominent bordered pits, but in addition they are sometimes broad and thin-walled and lie in radial series.

From these facts it is clear that the secretory reservoirs of the three genera in question always take the form of closed sacs, which De Bary has already pointed out as a feature of

certain Coniferæ (13, 440), and in order to clearly differentiate them from those which occur in the genus *Pinus* I shall reserve for all such cases the term *resin cyst*. While such cysts are typically developed in the three genera named, they are also features of *Pseudotsuga*, *Larix*, and *Picea*, — in fact, of all those genera in which the epithelium is composed of thick-walled cells, — but in these latter cases there is the additional feature that such cysts are always accompanied by the occurrence of similar structures in the medullary rays, and therefore they are associated with fusiform rays. From these facts, then, it is obvious that we have here a group of six genera all characterized by the presence of structurally similar resin reservoirs, but separable into two groups through the absence, on the one hand, and presence, on the other, of fusiform rays. That such saclike reservoirs represent the primitive form of the resin passage scarcely admits of question when we observe the various transitional forms which they present, and the relation which they bear to the resin passages of *Pinus*, — a view which is strengthened by the observation of De Bary (13, 443) that primitive forms of the secretory reservoir occur in the pith of *Gingko* in the form of elongated sacs.

De Bary has shown that (13, 440) the secretory passages traverse the wood longitudinally, at first as prismatic tubes, which usually acquire a round or elliptical transverse section. In its strict sense, this statement is applicable exclusively to the genus *Pinus*, but inasmuch as there are important structural gradations whereby *Pseudotsuga*, *Larix*, and *Picea* represent an intermediate type, while *Pinus* represents a completed type, it will be necessary to compare them somewhat in detail. In the genus *Pinus*, however, the secretory reservoir differs from that of all other genera, in that it consists of a definite and continuous canal of indeterminate length, and for the purpose of differentiating it from other forms I shall reserve for it the appropriate and long-used term *resin passage*.

In *Pseudotsuga* the resin cysts are always scattering, though they frequently occur in tangentially extended groups of two or

four contiguous or even coalescent reservoirs. The central canal, which is usually small and not infrequently very narrow, is rather more generally rounded than in previous types. The epithelium is very clearly defined and consists of one to three rows of thick-walled parenchyma cells, sometimes containing resin, the first row of which are rather small and radially flattened, but in *P. macrocarpa* they are rather thin-walled. In *P. Douglasii* the epithelium is commonly extended on the two sides of the resin canal in such a way as to form a tangentially elongated tract which not infrequently extends beyond and involves neighboring medullary rays. In *P. macrocarpa*, on the other hand, the epithelium is concentric with the canal, thus forming a tract of about equal thickness all around. Such a deviation as is expressed in *P. Douglasii* constitutes the first evidence of a tendency in development which is fully and frequently expressed in *Pinus*. Thyloses are of infrequent occurrence, and appear to be confined to *P. macrocarpa* where they are few in number and generally rather thin-walled. Parenchyma tracheids are usually not apparent in a transverse section. This results from the frequent location of the resin passage in the summer wood, which is not favorable to their development, and from the close resemblance which they bear to the tracheids of the spring wood; and while such elements form an integral part of the resin cyst, their particular disposition cannot be exactly defined, though there is no good reason for supposing that they differ in this respect from what may be observed in other cases. In a longitudinal section the canal is found to be more or less continuous, though it presents frequent constrictions and is thereby reduced to very narrow dimensions, or it may even be discontinuous and thereby form cysts. It is this feature which causes the canal to exhibit such marked variations in size, when seen in transverse section. The epithelial cells are narrowly cylindrical and rather long and thick-walled, as well as somewhat strongly pitted. Outwardly they become much longer and relatively narrower, and they eventually merge with the surrounding parenchyma tracheids, by which they may also be replaced (fig. 42).



In *Larix* the same features of contiguity and coalescence may be observed, except that in *L. occidentalis* the resin passages sometimes form into continuous zones of imperfectly organized structures with the aspect presented in *Tsuga Mertensiana*. The epithelium is always well defined (fig. 42), and it consists of one, sometimes two, rows of cells. The cells of the first row are

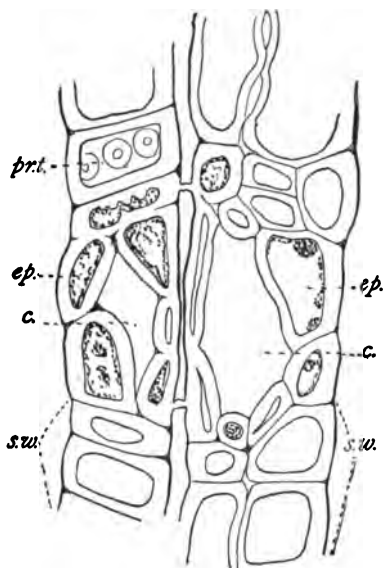


FIG. 42. *LARIX OCCIDENTALIS*. Transverse section from the inner spring wood showing a pair of resin passages with the central canals (*c.*); the thick-walled epithelium (*ep.*); a parenchyma tracheid (*p.r.t.*), and the summer wood (*s.w.*).  $\times 300$

small, very variable in form and size, thick-walled, and more or less strongly flattened radially. They are also commonly resinous and more or less strongly pitted. When there is a second row of epithelium the cells are essentially like the wood tracheids, and like the parenchyma tracheids, from which they may be separated with difficulty. The latter, therefore, which are absent from the summer wood, can be distinguished from the elements of the spring wood only when the pits on the terminal walls (fig. 42, *pr.t.*) are brought into view, or, more rarely, when the pits on the tangential walls are in evidence. Thyloses rarely occur, and so far they have been

noted only in *L. occidentalis*,

where they are infrequent and thick-walled, and in *L. americana*, where they are of rare occurrence and thin-walled. In longitudinal section the central canal is always continuous, though constricted at intervals, a feature in all essential respects the same as in *Pseudotsuga*. Radially the first row of epithelial cells are short cylindrical, or in *L. occidentalis* short fusiform, but there is a graduated increase in length outwardly, so that in the second

row, or in the third if present, they become narrow and very long, and they eventually blend with the parenchyma tracheids through intermediate forms with bordered pits. All of the epithelial cells are thick-walled and strongly pitted, and they thus offer a somewhat strong contrast to the rather thin-walled parenchyma tracheids with bordered pits.

The resin passages of *Picea* differ from those of *Pseudotsuga* and *Larix* in being more strictly segregated, and in consequence there is a conspicuous absence of contiguous structures, which may nevertheless sometimes be seen in *P. nigra*, and especially of coalescent forms. They are usually narrow, but well rounded or oval, and there is far greater uniformity of structure and form than in any of the preceding types. The epithelium consists of one row, one to two rows, or even one to three rows of cells,—differences which apparently belong to particular species, though no attempt has been made to define the precise limitations of

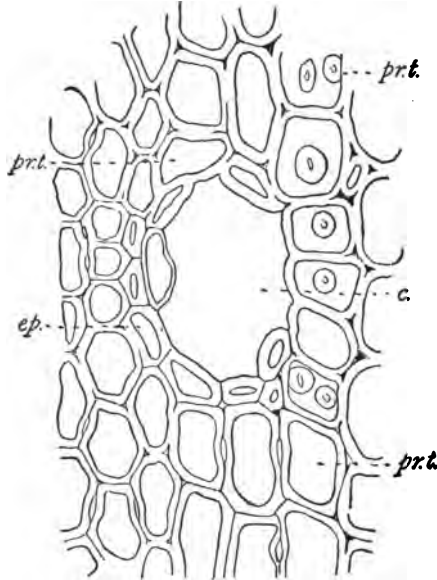


FIG. 43. *PICEA ALBA*. Transverse section of a resin passage from the spring wood showing the central canal (*c.*); the thick-walled epithelium (*ep.*), and the parenchyma tracheids (*prt.*).  $\times 300$

such features. The cells are generally small, round, or radially flattened and thick-walled, though occasionally a cell may be thin-walled, as in *P. alba*. In cases of thick-walled epithelium the outermost cells merge with similar tracheids, from which they are not readily distinguishable, while the general epithelium becomes extended into a tangentially elongated tract, as in *Pseudotsuga Douglasii* and *Pinus*. Occasionally thyloses have been

noted in *P. nigra*, *P. pungens*, and *P. sitchensis*, but they are always thin-walled. Parenchyma tracheids are not obvious in the summer wood, but they are recognizable in the spring wood, where they appear to replace the resin cells, though they are apparently of much less frequent occurrence than in the genera previously discussed. In *P. alba*, however (fig. 43, *pr.t.*), we sometimes find a radial series of tracheids which also extends laterally so as to form an inclosing layer. Longitudinally the canal is continuous, but with more or less frequent constrictions, as in *Pseudotsuga* and *Larix*. The epithelium consists of narrow cylindrical and much-pitted cells, which increase in length in the outer layers, where they become five to seven times longer than broad, and finally merge with the parenchyma tracheids, which replace them.

While the general composition of the resin passage in *Pseudotsuga*, *Larix*, and *Picea* is the same as that of the resin cyst, it is obvious that the frequent constrictions in the canal indicate a partial survival of the cystic formation. We must, therefore, regard these structures and the three genera to which they belong as forming a transition group between the primitive resin cyst, on the one hand, and the perfectly organized resin passage of *Pinus*, with its canal of uniform width, on the other.

In the genus *Pinus* the resin passages show considerable variation in detail, but they all conform to the same structural type (fig. 44). The central canal is broad and round, often very large, and in longitudinal section it is a perfectly continuous passage of uniform width. The epithelium consists of large but very variable and thin-walled cells in from one to several rows. In the soft pines it generally forms a concentric zone of uniform width, but in several of the hard pines there is a marked tendency to extension in a tangential direction and the formation of rather extensive eccentric tracts. In all of the pines there is a pronounced tendency for the epithelial elements to become so thin-walled that they are readily broken out in making sections, while in the hard pines, as *P. cubensis*, *P. tæda*, *P. pungens*, etc., the cells are often strongly resinous. In the outer epithelium the

thin-walled elements may be associated with occasional thick-walled elements with which they are interchangeable, precisely as in the similar relations displayed by the medullary rays of *P. pungens* and *P. cubensis*. In the same region also there is a similar association with and transformation into parenchyma tracheids, which also has its parallel in the medullary ray. Somewhat more specifically, special reference to two examples may

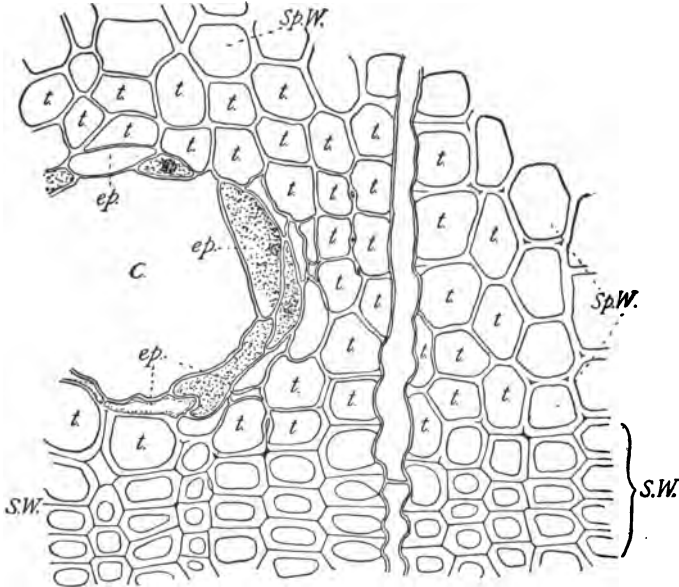


FIG. 44. *PINUS REFLEXA*. Transverse section of a resin passage from the inner face of the spring wood showing the central canal (C.); the thin-walled and resinous epithelium (ep.); the parenchyma tracheids (t); the spring wood (Sp.W.) and the summer wood (S.W.)  $\times 225$

serve to illustrate the general nature of some of the more important variations. In longitudinal section the parenchyma tracheids are usually of much greater length than the associated parenchyma cells, with which they are parallel or conterminous, and they occur in large numbers in *P. Lambertiana*. In *P. reflexa* they are conterminous with parenchyma cells, which they finally succeed, to be replaced in turn by thin-walled wood tracheids. In *P. Lambertiana* they are always to be distinguished by the

bordered pits on the radial, tangential, and terminal walls, while in *P. reflexa* they are characterized by the large number of bordered pits on the radial walls, with very few on the tangential walls. In the former situation the pits are much smaller than in adjacent wood tracheids. Together with adjacent wood tracheids the parenchyma tracheids may be more or less involved in bearing resin (*P. Lambertiana*), while finally, as exhibited in transverse section, their numbers may be so large that they form extensive areas about the resin passage (fig. 44). In such a case the sequence of elements in transverse section would be :

1. Canal with thyloses.
2. Thin-walled epithelium.
3. Epithelium and cylindrical parenchyma tracheids.
4. Parenchyma tracheids.
5. Wood tracheids with thin walls.

Thyloses are a constant feature in the structure of the resin passages of *Pinus* (fig. 31, *a*). They are always thin-walled and completely fill the canal. So constant are these features in association with those previously recounted that they serve to afford a ready means of accurately recognizing the genus under all circumstances.

The general course of development thus outlined shows that the parenchyma tracheid stands in such relation to the organization of the resin passage that its more frequent occurrence is directly correlated with a higher type of organization and development in the plants to which they belong.

We are now in a position to present a general summary of the relations which the resin cells bear to the organization of the secretory reservoirs — cysts and passages — and the position which the latter occupy in the economy of the plant as follows :

1. Resin cells, which are of the nature of wood parenchyma, at first occur as isolated structures filled with resin, but they show a definite tendency to association and later form definite aggregates.
2. Parenchyma tracheids become associated with such aggregates for the purpose of effecting a more complete nutrition of the secretory cells.

3. Resin cells when aggregated beyond a certain point develop schizogenous intercellular spaces, which form either central closed cysts or central canals of indeterminate length.
4. The structure of the cyst or passage always presents the same sequence of elements, and the work of the reservoir is then divided between
  - a. the tracheids, which provide nutrition for the secretory cells;
  - b. the secretory cells or epithelium, in which the formation of the resin takes place;
  - c. the cyst or canal, which provides an outlet or storage reservoir for the surplus product;
  - d. the thyloses, which may impede the proper storage of the resin, or which may individually serve the purpose of storage.

So long as the formation of resin is not excessive it is stored in the cells where produced. This is true of all isolated resin cells as well as of many which enter into the composition of complex cysts and passages. When the resin is excessive, however, the surplus is excreted into specialized reservoirs of the form of closed cysts or of canals, and we are led to interpret the appearance of these structures in the higher Coniferæ as a response to such needs. The development of the resin passages will thus be seen to stand in direct relation to the capacity of the plant as a resin producer, — a fact which is otherwise apparent from our knowledge of the general capacity of the different genera as resin producers, and from a comparison of this feature with their known position in the line of descent.

## CHAPTER X

### RESIN PASSAGES (*continued*)

#### DISTRIBUTION AND PHYLOGENY

Prantl (62, 37) states that resin passages occur in the wood of "most Abietineæ, namely, *Pseudotsuga*, *Picea*, *Larix*, *Pinus*, and *Abies firma*." This statement requires some modification in detail, especially with respect to the last-named genus, and in order to make the results of the present studies clear it will be expedient to discuss separately the distribution of the resin cysts and the resin passages.

The first species to which our attention may be directed is *Tsuga Mertensiana*. This is the only species of the genus in which definite resin cysts are to be found. Such structures are never numerous, and they take the form of short rows of contiguous cysts in the initial layer of the summer wood of distant growth rings. Longitudinally they have no definite limits, but they appear to be extended for great distances, and probably through the entire longitudinal growth of the season, at least. There is no obvious alteration either in the position or volume of the resinous contents of the isolated resin cells which lie on the outer face of the summer wood. The constancy with which these structures occur gives to them a definite value for the recognition of the species, and permits us to differentiate it from *T. caroliniana* on the one hand, and from the remaining three species on the other.

In the genus *Abies* only four species out of eleven show resin cysts. These are *A. bracteata*, *A. nobilis*, *A. concolor*, and *A. firma*. Referring again to Prantl's observation (62, 37), it must be pointed out that his statement with respect to the occurrence of resin passages in *A. firma* requires modification in

detail, in so far as these structures are not passages but cysts; while he also appears to have overlooked the occurrence of similar structures in the three other species mentioned. In all of these cases the cysts are contiguous and disposed in tangential rows of considerable length, either in the summer wood (*A. concolor* and *A. nobilis*), in the outer spring wood (*A. firma*), or in both the spring and summer wood (*A. bracteata*). Such variations appear to be of no specific value, conforming as they do to similar variations in the zonate distribution of the resin cells. It is found, however, that in only one case (*A. concolor*) are these cysts associated with isolated resin cells. In the three other cases the resin cells are entirely wanting, — a relation which is strongly suggestive of their replacement by the cysts.

*Sequoia sempervirens* is the only species of that genus which develops resin cysts in the secondary wood, though Jeffrey (24) has shown that such structures are normal to the primary wood zone of *S. gigantea*, and not elsewhere. As already shown, such cysts are much more highly organized than those of either *Tsuga* or *Abies*, though they are similarly contiguous and even coalescent, and form extensive tangential rows in the initial layer of the spring wood of distant growth rings. They form a much more prominent feature than in any of the preceding species because of their generally larger size and the greater extent of the series in which they lie. Unlike *Abies*, however, there appears to be no diminution either in the number or the extent of the prominent resin cells, which are often intimately associated with the cysts.

The normal course of development for such cysts as are thus described is subject to special alteration under conditions which involve an unusual stimulus to growth, and under such circumstances they may become definitely associated with, or may even be regarded as indicative of, pathological conditions. Thus Anderson (1, 28–29) has shown that such cysts are definitely developed in association with the formation of witches' brooms in *Abies firma*. Under such circumstances the cysts become much larger, more distant, and more numerous than in normal growth, but they form well-defined tangential rows in the earlier



spring wood of successive growth rings. In the development of such secondary features the cysts manifestly exhibit a distinct approach to that higher type of structure and distribution which is exhibited in *Picea*. In the following year Anderson (2, 336) further showed that, while resin cysts are absent from the normal wood of *A. balsamea*, they do arise under the influence of the special stimulus connected with the formation of tumors produced by the action of *Æcidium elatinum*. He furthermore points out that such cysts attain their greatest development and largest number in the region of greatest stimulation, i.e. in the middle of the tumor,<sup>1</sup> decreasing above and below until they eventually become pointed and finally disappear between four tracheids "which, in their meristematic condition, probably function as epithelial cells." It is unfortunate that the histological details of these cysts and their endings are not given, since such facts would serve to throw much light upon the relation of the cysts to similar structures in normal tissues, but there is no reason to suppose that they differ in their essential structure from those which occur in the normal tissues of the same or other species. The tracheids above referred to are undoubtedly parenchyma tracheids, and it is probable that further examination would show that they ultimately replace the resin cells remaining over after the disappearance of the cyst proper.

Tubeuf has also shown (72, 44) that resin canals are irregularly formed and greatly multiplied through the action of parasites, quoting the case cited by Hartig in which the resin canals of the spruce were found to be so numerous in trees attacked by *Agaricus melleus* as to give rise to an abnormal production of resin, which flows from the roots and characterizes the disease called *resin gland* or *resin flux*. He also points out that a similar flux occurs in the bark of the pine, due to the action of *Peridermium pini*. The action is therefore developed in such a way as to induce a greater activity in the formation of wood parenchyma, which, in *Juniperus communis*, when attacked by

<sup>1</sup> A precisely similar relation in development has been noted by Jeffrey (25) in the case of *Sequoia Penhallowii*.

*Gymnosporangium clavariæforme*, often forms somewhat extensive wedge-shaped masses projecting between the rows of tracheids (72, 388). A close comparison of such a tissue with that of the resin cysts of *Abies* shows that the two are essentially the same, and we must therefore conclude that the cell aggregates which precede the formation of resin cysts in *Sequoia*, *Abies*, etc., are also to be found in *Juniperus* as a consequence of injury effected by parasitic growths.

More recently Jeffrey (24) has contributed an important paper on the anatomy of *Sequoia*, in which he brings out several facts of considerable value. He shows that resin cysts may arise in the roots of *Abies balsamea* which have been injured, while they may also be produced experimentally by injury, thus confirming the observations of Anderson that they may be traumatic in their origin. The most significant facts, however, relate to the normal occurrence of such cysts in *Sequoia*. He shows in the first instance that they are absent from the wood of the first year's growth in *S. sempervirens*, while they are present for the same period of growth in *S. gigantea*, though absent from the growth of later years. In both species they arise in the earlier spring wood. In the case of *S. Penhallowii* from the Miocene the same author directs attention (25) to the occurrence of resin passages in both a radial and longitudinal direction, and establishes important relations between them. The somewhat strict localization of the latter and their obvious connection with injury in well-defined instances leads him to the conclusion that they are wholly traumatic. This rule he also applies to all cases of tangentially disposed resin cysts or resin passages such as occur in *Sequoia sempervirens*, thereby making it include all similar cases in the various species of *Abies* and *Tsuga*.

Some years since, De Bary (13, 490-495) formulated the law that "resin canals occur in the ligneous bundles of the same *Abietineæ* which possess horizontal canals in the medullary rays." This is a law of very great constancy in all those cases in which a canal proper is developed, though it fails in such cases of resin cysts as occur in *Abies* and *Tsuga* (59). It also

fails in the case of *Sequoia sempervirens* and *S. Langsdorfii* (46), and it likewise appears to fail in the case of *S. Burgessii*, but in this latter case it is possible that there is the same peculiarity of distribution which Jeffrey has observed in *S. Penhallowii*, according to which local areas may be devoid of longitudinal canals while radial ones may be present.

As presented by existing species, *Pseudotsuga*, *Larix*, *Picea*, and *Pinus*, without exception, show resin passages in both the radial and longitudinal positions. In transverse section they are scattered throughout, sometimes appearing chiefly in the summer wood, sometimes chiefly in the spring wood, or again about equally in the two regions, and they rarely conform to the precise law stated by De Bary (13, 495) that "they lie scattering in a ring in the external region of every annular layer." The constancy of their occurrence in the four genera mentioned involves very few features which call for special comment. In *Pseudotsuga* and *Larix* the resin passages are scattering. They sometimes unite in pairs so as to form short tangential series, and they thus approach the type of *Tsuga* or *Abies*, while yet again they may become definitely isolated and scattering, thereby approaching the distribution of *Picea* and *Pinus*. In *Larix occidentalis* the tendency to a primitive form of distribution is expressed in the formation of a tangential zone essentially similar to that of *Tsuga Mertensiana*. In both *Pseudotsuga* and *Larix* there is an obliteration of resin cells from all parts of the structure except the extreme outer face of the summer wood. In *Picea*, however, without exception, there is a complete obliteration of all resin cells except such as enter into the structure of the resin passages, and this is directly correlated with a higher type of structure in such passages.

In the genus *Pinus*, as already shown, the resin passage reaches the highest degree of organization in all respects. It shows little if any tendency to those primitive associations which are expressed in the formation of tangential series, while it has entirely replaced the isolated resin cells, which are never to be found in that genus.

If, then, we ask what value such structures have for taxonomic purposes, we find them to be of well-defined importance. It has already appeared that in *Tsuga* the occurrence of resin cysts is of well-defined value for specific differentiation, and the same rule is also applicable to *Sequoia sempervirens* and to four species of *Abies*. In the higher *Abietineae*, inclusive of *Pseudotsuga*, *Larix*, *Picea*, and *Pinus*, the invariable association of resin passages in the wood and in the medullary rays not only serves to separate these genera from all those in which resin cysts only may occur, but it also differentiates them absolutely from all the remaining genera. Such association, therefore, constitutes a feature of great value. More particularly, the thin-walled epithelium of *Pinus* at once separates that genus from the other three, which are invariably characterized by thick-walled epithelium. Such generic differentiations are greatly emphasized by the occurrence of thyloses. These are typically developed in *Pinus*, where they are always thin-walled and almost invariably present. They are, therefore, of definite value as supplementing other features previously described. In the other genera, however, their presence in either the cyst or the resin passage, where they are generally thick-walled, is of so sporadic a nature as to give them no definite value, and we therefore find that for specific diagnoses such structures may be neglected.

We are now in a position to present an answer to the question, How are the resin passages related to the phylogeny of the *Coniferales*? In order to present an intelligent answer to this question, it will be necessary to recall the facts already discussed in connection with the resin cells, and bring them into relation with our discussion of the resin passages.

In the genus *Sequoia* it has been shown that the general course of development of the resin cells is essentially the same as in *Cupressus*, etc., while it has also been shown that the genus presents in other respects a somewhat remarkable deviation. Of the two existing species both show the distribution of the resin cells to be of the typically primitive form, i.e. scattering. Nevertheless there are also in *Sequoia sempervirens* definitely

organized resin cysts, but without exhibiting the transitional form of a zonate disposition. Among fossil representatives Penhallow (46, 41) has shown precisely the same feature to be present in *S. Langsdorfii*.<sup>1</sup> This is the less remarkable, however, because that species is undoubtedly the ancestral form of, and practically identical with, *S. sempervirens*. The fact made clear by Jeffrey (24, 457) that resin cysts occur in the first annual ring of vigorous branches of adult trees, as well as in the roots of *S. gigantea*, also tends to make it apparent that the genus presents a very striking advance upon even the type exhibited by *Juniperus*, since the aggregation of resin cells and the formation of cysts from them has arisen abruptly, and without the transitional forms presented by *Juniperus* and *Taxodium*. While, therefore, *Sequoia* is obviously related to *Thuya* and *Cupressus*, on the one hand, it is, on the other hand, related to such types as *Abies*.<sup>2</sup> In this sense it may be regarded as the terminal member of a developmental series embracing the *Taxodiinae*, *Cupressineae*, *Taxoideae*, as follows:

- |                                      |                        |
|--------------------------------------|------------------------|
| 1. <i>Taxus</i> and <i>Torreya</i> . | 6. <i>Thuya</i> .      |
| 2. <i>Thujaopsis</i> .               | 7. <i>Libocedrus</i> . |
| 3. <i>Cryptomeria</i> .              | 8. <i>Taxodium</i> .   |
| 4. <i>Podocarpus</i> .               | 9. <i>Juniperus</i> .  |
| 5. <i>Cupressus</i> .                | 10. <i>Sequoia</i> .   |

In the *Abietineae* a new series is presented. This is not in any sense strictly conterminous with the first, but the two appear to make a fault, as it were, whereby there is a lateral displacement, but of such a nature that *Sequoia* still serves as the connecting link. Within the eleven species of *Abies* investigated three important phases are presented, — (1) resin cells scattering on the outer face of the summer wood, (2) resin cells grouped and forming cysts, and (3) resin cells entirely wanting. Viewing these phases in the order given, it is to be observed that in those

<sup>1</sup> While Jeffrey has shown (25) that in *S. Penhallowii* the resin cells are normally confined to the outer face of the summer wood.

<sup>2</sup> This latter relation has been recently emphasized by Jeffrey (25) through studies relating to *S. Penhallowii*, and it is in direct confirmation of conclusions already reached by Penhallow (44) on the basis of other data.

four species which develop cysts only one shows isolated resin cells, and it is probably correct to interpret the variations noted as expressions of developmental phases in such a way that the occurrence of cysts represents the highest position. The genus *Tsuga* is closely related to *Abies* in the occurrence of isolated resin cells on the outer face of the summer wood, as also in the formation of resin cysts, but it obviously occupies an inferior position because (1) of the greater abundance of resin in the individual cells, and (2) the occurrence of definite aggregates of resin cells without the formation of cysts. This series is directly extended by those genera in which definite resin passages replace the simple cysts, since the latter are convertible into the former by easy and natural transitions. Both *Pseudotsuga* and *Larix* occupy equivalent positions because they not only present resin passages of an equal degree of development, but they also show a survival of the isolated resin cells on the outer face of the summer wood. Their affinities are therefore directly with *Abies* and *Tsuga* on the lower side, but on the upper side their alliance is with *Picea*, which presents a very similar though somewhat higher organization of the resin passage and a complete obliteration of the isolated resin cell. Yet again, the structure of the resin passage in *Picea* at once connects that genus with *Pinus* in which the most complete development is attained, and it therefore terminates the series upwardly.

Having special reference to the particular forms of the secretory reservoirs, and leaving out of account all other considerations than their particular evolution, it is possible to indicate the general sequence of the genera, and, to a more limited extent, of their species, as follows :

- |                               |                             |  |
|-------------------------------|-----------------------------|--|
| 1. <i>Tsuga caroliniana</i> . | 2. <i>Abies bracteata</i> . | 3. <i>Sequoia</i> .                      |
|                               | <i>Abies firma</i> .        | 4. <i>Pseudotsuga</i> and <i>Larix</i> . |
| <i>Tsuga Mertensiana</i> .    | <i>Abies nobilis</i> .      | 5. <i>Picea</i> .                        |
|                               | <i>Abies concolor</i> .     | 6. <i>Pinus</i> .                        |

From this it is manifest that *Sequoia* is superior to *Tsuga* and *Abies*, but inferior to *Pseudotsuga*, *Larix*, etc. But if we now view the general phylogeny with reference to the entire course

of development of the resin cells and the resin passages, the relations just explained must be modified with reference to the particular position of *Sequoia*, and the sequence would then become:

- |                         |                        |                            |
|-------------------------|------------------------|----------------------------|
| 1. <i>Thujopsis</i> and | 5. <i>Libocedrus</i> . | 10. <i>Abies</i> .         |
| <i>Cryptomeria</i> .    | 6. <i>Taxodium</i> .   | 11. <i>Pseudotsuga</i> and |
| 2. <i>Podocarpus</i> .  | 7. <i>Juniperus</i> .  | <i>Larix</i> .             |
| 3. <i>Cupressus</i> .   | 8. <i>Sequoia</i> .    | 12. <i>Picea</i> .         |
| 4. <i>Thuja</i> .       | 9. <i>Tsuga</i> .      | 13. <i>Pinus</i> .         |

But it may assist in the general argument to view this question from another standpoint. Regarding the resin cells and the secretory reservoirs as falling within a definite series, we may apply to the various forms of distribution, and to the various grades of resin reservoirs, arbitrary values of such a nature as to represent our conception of their relative positions in the scale of development as expressed by percentages, thus:

Resin cells scattering . . . . .	25.0%
Resin cells zonate . . . . .	37.5
*Resin cells grouped . . . . .	50.0
Resin cells on the outer face of the summer wood, as in	
<i>Pseudotsuga</i> and <i>Larix</i> . . . . .	12.5
Resin cells on the outer face of the summer wood, as in	
<i>Abies</i> (partial only) . . . . .	5.0
Resin cells wholly wanting . . . . .	0.0
†Resin cysts, as in <i>Tsuga</i> , <i>Abies</i> , and <i>Sequoia</i> . . . . .	70.0
Resin passages with constrictions, as in <i>Pseudotsuga</i> , <i>Larix</i> , and <i>Picea</i> . . . . .	80.0
Resin passages without constrictions and of the highest type of organization, as in <i>Pinus</i> . . . . .	100.0

We obviously have two subordinate series here, which for convenience may be regarded as conterminous, but which, as already shown, are "faulted" in such a way that the grouped resin cells (\*) and the resin cysts (†) jointly represent the point of divergence for two separate courses of development, the latter continuing upward, while the former descend and thereby represent degradation. These features are best exhibited graphically, and the accompanying curves clearly show how, on the one hand, resin cysts and resin passages directly result from

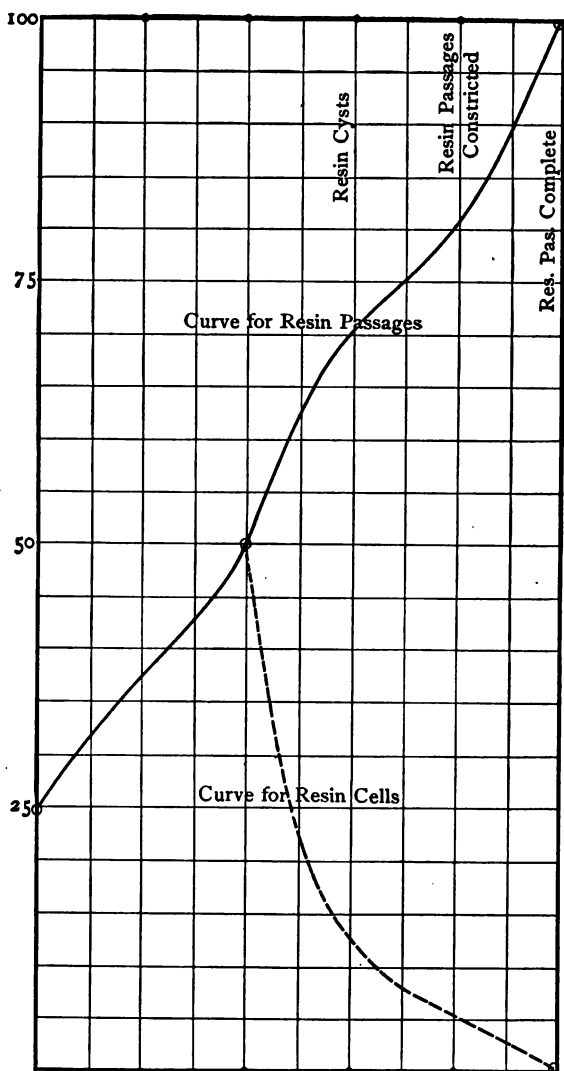


FIG. 45. Curve showing the approximate development of resin passages and the corresponding obliteration of resin cells



special modification of cell aggregates, while, on the other hand, from the same starting point, there arises a course of degradation which finally results in the complete obliteration of the resin cell as an independent structure.

The facts thus far set forth have thrown important light upon the general course of development of certain anatomical features, and they also show the general course of development for genera and species with reference to particular structures. They do not, however, convey any information with respect to the origin of the phylum as a whole, or the relations of the particular genera and species from the standpoint of collective data, and such a discussion will be more appropriately reserved for the general summary. There is, however, one feature arising out of recent investigations which calls for consideration at this point, since certain of the conclusions reached are not in harmony with our own, the divergence of opinion indicated being the result of different methods of interpretation.

Jeffrey states (24, 447, 457) that all such resin cysts as occur in *Sequoia sempervirens* and *Abies* are of a traumatic nature, and therefore pathological. To this category he would also doubtless assign the corresponding structures of *Tsuga*. This opinion appears to be shared by Anderson (1, 2), and it is also apparently supported by Pierce (60). Both Jeffrey and Anderson show that the development of such cysts is sometimes definitely associated with the production of tumors through the operation of parasites, and that they may also be induced by wounds experimentally produced. The facts they cite show conclusively that resin cysts may and often do arise traumatically, and such is unquestionably true of *Sequoia Penhallowii*, as shown by Jeffrey (25) within the limits of our present knowledge of that species, but in such cases they lie outside the usual course of development.

The occurrence of resin passages in the fundamental tissue of the Coniferales is a well-known fact, as pointed out by De Bary (13, 441) many years since, when he summarized the general facts in the statement that "all investigated species of Coniferæ,

with the single exception of *Taxus*, have resin passages or resin reservoirs, which vary in distribution and number according to the species." This statement would include the leaves and bark, and sometimes even the pith of species which produce neither isolated resin cells nor resin reservoirs of any kind in the xylem tissue of the stem. It directs attention somewhat forcibly to the fact that while the occurrence of resin reservoirs in the fundamental tissue is a legitimate inheritance of the mucilage canals of the Eusporangiate ferns and the Cycadofilices, as also later of the resin cells of Cordaitales, the xylem structure is the very last to receive the impress of such a course of development; and it is therefore in nowise surprising that the resin passages do not appear there until a very late period of development, and that their organization can even then be brought about only through a somewhat prolonged series of changes which are initiated by the occurrence of isolated resin cells, much as the formation of mucilage canals may be traced back to specialized cells which separately have the same function in the Eusporangiate ferns.

The local occurrence of resin passages in the xylem of the floral axis in no way invalidates the obvious conclusions to be drawn from these statements, since it may be readily accounted for in other ways. In a structure so unresponsive to influences which would induce profound alterations as the xylem, it is to be expected that important structural changes could be effected only after a prolonged interval during which the fixation of any particular character would be preceded by a period of sporadic development, within which such character would be liable to recur under special conditions; and as such conditions are obviously of fundamental importance, we may inquire somewhat more fully into their nature and results.

The statement of Prantl (62, 35), that "Those genera which are devoid of resin passages in the wood of young and vigorous growth later produce single parenchyma elements in the wood which contain resin," requires some modification in view of what Jeffrey has shown in the case of *Sequoia* and *Abies*, as well as

what has been shown in the course of the present studies, and in its more comprehensive and exact form it should read, "Those genera which are usually devoid of resin passages in the wood, but some species of which may nevertheless contain resin cysts in the young and vigorous growth, later produce single parenchyma elements in the wood which contain resin."

Taken by itself, this statement as applied to *Sequoia* and *Abies* might be held to indicate that the growth of the first year represents the most stable structural region of the entire stem, in the sense that it embodies characters which are most fully established, and that it will therefore embrace elements which may be eliminated from the older parts, or which may be replaced there by degenerate forms only. From this point of view it would be necessary to regard the complex resin passage as the primitive form of structure from which the cysts, groups of cells, and isolated resin cells have been derived by a process of progressive degradation. This view appears to have been adopted by Jeffrey (24, 454), who supports his position by citing the occurrence of resin passages in the vascular structure of the peduncle of certain fossil Cycads, interpreting this to mean that such structures represent a survival of features which have been obliterated from the structure of the stem. Such a view does not seem to be in harmony with the facts which our own studies have brought out, to the effect that resin passages of the type found in the xylem structure are in no sense primitive or vestigial, since they are wholly wanting in the primitive gymnosperms, and their organization does not arise until a very late period in the evolution of the higher forms. If our interpretation of observed facts is correct, as applied to the origin of the resin passages, it shows as clearly as one could well expect a progressive development from the isolated resin cell through various phases of aggregation to the highest form of structure as found in *Pinus*. That there is such a series cannot be doubted, and we must interpret it in one of two ways, — either as progressive evolution or as progressive degeneration. To us the arguments all seem to be very emphatic with respect to lending support to

the former view, most especially as all anatomical data confirm the relative positions of the genera as determined by the development of the resin passage. But assuming for the moment that the latter view is the correct one, let us see where it would lead us. It would, first of all, necessitate a direct reversal of the structural sequence, and this in turn would impose the necessity of placing the genus *Pinus* at the bottom of the scale, while those genera, like *Taxus*, *Torreya*, *Dammara*, etc., which have no resin cells even, would be at the top. I venture to suggest that such a proposition would meet with instant opposition, even from the advocates of the idea that the resin passage has preceded the other forms of resin-bearing structures. The whole question appears to turn upon our recognition of what constitutes the most impressionable portions of the stem structure, and therefore the regions within which structural changes are initiated. In this connection the evidence of both paleobotany and recent botany brings out certain facts with great force and throws them into strong relief. They are as follows :

1. The mucilage canals of the Eusporangiate ferns may be regarded as the ancestral forms of the resin passages among the higher plants, but they are obviously the successors of, as they are derived from aggregates of, mucilage sacs as simple parenchyma cells.

2. Resin passages are wholly unknown in the wood of the stem of ferns, the Cycadofilices, the Cycads, Cordaites, or Araucarioxylon.

3. Resin cells are known and are abundant in the pith and bark of Cordaites, but they are absent from its wood.

4. Resin passages are known in the bark and in the pith of the Cycadaceæ, of *Dammara* and *Araucaria*, and of the Coniferales in general. They also occur in the wood of the peduncles of *Sequoia* and in the xylem of the first year's growth of vigorous shoots in *Sequoia* and *Abies*. They likewise occur in the leaves generally.

5. In *Sequoia Burgessii*, from the Eocene, resin passages occur in the medullary rays, but they do not traverse the wood longitudinally, though isolated resin cells do occur there.

From this it would seem that the fundamental tissue is the most impressionable with respect to the development of these structures, and that after it we have in the same order the peduncle of the inflorescences and the wood of the young shoots, to which latter category would also belong the development of resin passages in fasciated stems, and such a sequence is precisely what we should expect from our knowledge of the relation which the fundamental tissue bears to other structures. According to this conception the resin passages may appear in any part of the woody structure where growth is sufficiently vigorous, but such appearance would be temporary and indicative only of a future course of development which has not as yet become sufficiently well impressed upon the organism to form a permanent feature of it. In other words, the tissue exhibits what in other cases would be termed "sports." Such structural forecasts are well known and of frequent occurrence. As applied to the development of tissues, no better example is afforded than that shown by the central strand of mosses, which is generally accepted as prophetic of the future vascular system in the sporophyte, and they serve to suggest that the law of mutation as proposed by De Vries finds expression in the evolution of internal structures as well as in the development of external forms. Such cases as *Sequoia gigantea*, which shows resin cysts in the wood of the first year and nowhere else, being replaced later by resin cells, appear to us to show that young and vigorous growth in general, and therefore the growth ring of the first year, constitutes a transitional zone within which many changes of structure wholly apart from the strictly normal may arise; and such a law would similarly be applicable to the wood of peduncles. This feature is manifested in the structure of the medullary ray, the character of the tracheids as exhibited in transverse section, the genesis of the bordered pits from spiral tracheids, and, in all probability, also in the formation of resin passages in *Sequoia* and *Abies*, as noted by Jeffrey.

Changes of this nature are to be regarded as tendencies in development in the direction of higher types of structure, whereby

potentialities assume a more or less definite form. From this it may be assumed that the primary growth ring is a zone within which sporadic characters are common, but it is only in the later rings that the various anatomical characters become permanently developed and properly express the normal features of structure and development.

The considerations dealt with here, as well as in previous chapters, lead us to give renewed emphasis to a view which has been expressed elsewhere, and which finds justification in many ways, not only in the gymnosperms but in the *Salicaceæ* and in *Catalpa* among the angiosperms, to the effect that inasmuch as the physiological activity of the plant is directly associated with and dependent upon conditions of internal structure, variations in the internal anatomy are to be regarded as of primary importance, and such changes are no doubt established or may be established considerably in advance of corresponding alterations in the external character of the vegetative or even of the reproductive organs. From this point of view questions of internal structure must always have precedence over those of external morphology in questions of classification.

## CHAPTER XI

### GENERAL PHYLOGENY

The results to which we are now brought are based entirely upon developmental phases in anatomical elements of the vascular cylinder. While our studies lead to certain definite conclusions, we do not in any sense regard these as final, but only as affording one step in the solution of a question which must be viewed not only from the broader standpoint of more extended anatomical data but also from that of physiology as well, although we feel disposed to insist that the final answer will be found to rest chiefly upon an anatomical basis. That there may be room for a different interpretation of the facts here recorded is quite possible, since Dr. Jeffrey has recently permitted me to examine the manuscript of an important contribution to our knowledge of the *Abietineæ*, in which he brings out very significant facts, which suggest that the group is of a much more primitive character than has hitherto been supposed or than is indicated by our own studies. It is therefore of importance that final judgment should be suspended until the results of these various studies, as well as those of Coulter, Chamberlain, and Ferguson, all directed to the same end but prosecuted along somewhat different lines, can be brought together and coördinated. It is in this sense that the following conclusions are offered.

In discussing the phylogeny of the higher gymnosperms three subordinate phyla must be taken into consideration in the following order: (1) *Cordaitales*, (2) *Gingkoales*, (3) *Coniferales*.

Regarding the *Cordaitales* as the most primitive gymnospermous stock of which we have present knowledge, it is possible to trace its origin to the *Cycadofilices*. The genera *Lyginodendron*, *Heterangium*, and *Calamopitys* present many structural features which are common to all, and which not only establish their

relation to the Cycadean line of descent but also offer many suggestions of that course of development which is realized in the higher Coniferales. They therefore constitute the real starting point for two lines of descent, the first of which embraces the Cycadales. At the present moment we have little or nothing to do with this beyond establishing its probable relation to the other gymnosperms. The second line emerges in a type of plants having characteristics distinctly allied to those of the Coniferae, and it is this line of descent with which we are now chiefly concerned. It is now possible to define the origin of this phylum somewhat more exactly than Coulter has done (11, 12), since there is good reason to believe that it emerges from the Cycadofilices through Poroxyton. Scott (81, 398) has already pointed out the relations of this genus to the Cycadofilices and the Cycadaceae on the one hand, and to Cordaites on the other, so clearly as to remove the necessity for detailed discussion at this time, beyond giving emphasis to one or two important structural relations. In *Calamopitys saturni* it has been noted that the most primitive distribution of the bordered pits upon both the radial and tangential walls is represented in the protoxylem structure. Such distribution, however, undergoes rapid modification whereby it is wholly limited to the radial walls in the secondary wood. A similar limitation appears in other somewhat closely related genera, and it is fully expressed in Poroxyton, where the multi-seriate disposition and hexagonal form are typically preserved, though there is at the same time a tendency to segregation to such an extent that the pits sometimes become round. In this it is possible to notice the first indication of a character which, while infrequent, is nevertheless occasionally expressed among the Cordaitales, though it is generally characteristic of the related phyla, Gingkoales and Coniferales.

Among the Cordaitales there is but one genus (*Cordaites*) which we have heretofore been accustomed to associate with that phylum, and, so far as our present knowledge goes, it undoubtedly stands in the closest relations to Poroxyton. It is, however, improbable that the two were in any sense conterminous, and it is altogether



probable that there may have been some one or more intermediate forms of which we have no present knowledge. Our present studies, on the other hand, show clearly that we must bring into this phylum two other genera of an obviously higher degree of development, but which have commonly been ranked with the Abietineæ and which, according to Eichler (15), occupy the highest position in the scale. This position is untenable upon anatomical grounds which give us reason to believe that *Dammara* and *Araucaria* (including, of course, *Araucarioxylon*) are not only inferior to the Coniferales as a whole but that they are also distinctly Cordaitan. Accepting this view and the fact that *Dammara* is the inferior genus, the sequence would place *Cordaite*s at the base and *Araucaria* at the top, with *Walchia* as the immediately ancestral form of the latter. This relation is not only natural but it is justified on anatomical grounds.

The tendency to segregation of the bordered pits, as exhibited by *Poroxyton*, suggests the relation of this genus to others in which such a feature is fully expressed, and it thereby forms the basal member of another series. From the opposite point of view it has been shown that the occurrence of two-seriate pits in *Pinus* and others of the Coniferales, as well as in *Ginkgo*, points to a common origin for such genera in a type with multiseriate hexagonal pits, and that both *Dammara* and *Araucaria* must likewise center in the same generalized form. This gradual convergence is justified on other grounds, and the genus *Poroxyton* among known forms most nearly fulfils the requirements of the case. We may therefore look upon it as lying between the Cycadofilices and all the higher gymnosperms, giving rise to two lines of descent, the first of which embraces the Cordaitales, as already described, while the second shortly divides once more. This secondary division gives rise on the one side to the Ginkgoales, and on the other to the Coniferales. The anatomical data already discussed, when viewed collectively, show that the general sequence within the latter would be (1) the Taxoideæ, (2) the Taxodiinæ, (3) the Cupressineæ, (4) *Abies*, (5) *Tsuga*, (6) *Pseudotsuga*, (7) *Larix*, (8) *Picea*, and (9) *Pinus*, of which one division, (II), represents the highest

type of development. With respect to the precise position of *Sequoia* in particular, its relation to *Abies* on the one hand, and to such genera as *Thuja* and *Cupressus* on the other, cannot be taken, in the present state of our knowledge, to indicate its origin from or its ancestry to either of them. The facts derived from anatomy, however, do indicate a more or less common origin for all four genera, and from this point of view, taking into account the peculiar features exhibited by *Sequoia*, they would seem to justify the idea that that genus represents a short side line of development, which does not lead to the evolution of other types, but terminates in *S. gigantea* after a comparatively brief period. The sequence of species for each genus cannot always be determined with a full measure of satisfaction, and these difficulties may possibly be made clear by reference to the succession of the two species of *Sequoia*, which is difficult to determine on purely anatomical grounds, but the general tendency of the facts already recited is to give to *S. sempervirens* the more primitive position, — a view which is sustained by its paleontological history.

The relations brought out in the foregoing studies, and the reasons for the conclusions reached, may be made more obvious, without the tedious method of a detailed discussion, by reference to the accompanying table of anatomical data (Appendix A), which substantially summarizes all the results derived from the study of particular structures. In preparing this table the various anatomical features have been chosen with reference to (1) the constancy of their occurrence, (2) their structural prominence, and (3) their obvious relation to diagnostic purposes. In their horizontal extension an attempt has been made to arrange them in accordance with the law of frequency, as well as with reference to their relation to development, in such wise that while the spiral tracheid is assumed to be the most primitive type of the vascular structure, the presence of two kinds of cells in the medullary ray may be held to express the highest form of development. To the members of the series so constituted we may then assign arbitrary values in arithmetical sequence from one to seventeen; while those subordinate characters which are represented by

different forms of distribution may be regarded as forming a second series similarly valued. Any primitive or other character which has become obliterated through development may be held to retain its original value with respect to the general course of such development, and it is always indicated by —. Vestigial structures occurring sporadically are designated by 1, and to them one half the value of the fully developed character is assigned. All normal features are designated by x, which becomes  $x +$  when they show development toward the next higher form, or  $x -$  when they show a definite tendency to degeneration. Sporadic characters which are obviously in the line of development are indicated by o, but they are assigned only half values. On this basis it is possible to arrange a sequence of genera and species in such a manner as to exhibit a progressive development from the simple *Dammara*, with a minimum of characteristics, to the complex *Pinus*, in which the greatest number of anatomical features is involved. Furthermore through such a series it is possible to determine the relative position of the various genera by percentage values, and it gives the most valuable insight into the approximate relations of the various members within the general line of descent. Such relations are determined not only for each anatomical character but also for the collective characters. Reducing these facts to a graphic form, the accompanying curves will assist in making the relations more clear, especially in emphasizing the general course of development, and, in their final form, they are best expressed by a biological tree. A figure of this sort is difficult to construct, and there is no agreement among investigators as to the particular form it should take. While the figures in common use indicate a certain relationship in descent, they completely fail to convey any impression of the way in which the succession arises, and they furnish no indication of possible gaps. They therefore constitute a very poor working basis.

In teaching I have long been accustomed to compare the various lines of descent among plants with the branchings of a deliquescent tree, since it has always seemed reasonable to

suppose that the laws which govern the branching of a limb, which give rise to all the varying forms of arrested development, and which thereby determine a particular modification of the figure which would otherwise result from unmodified growth, must be equally applicable to the general evolution of the higher forms of plants from a common ancestral type. In endeavoring to secure a natural growth which would best express all the

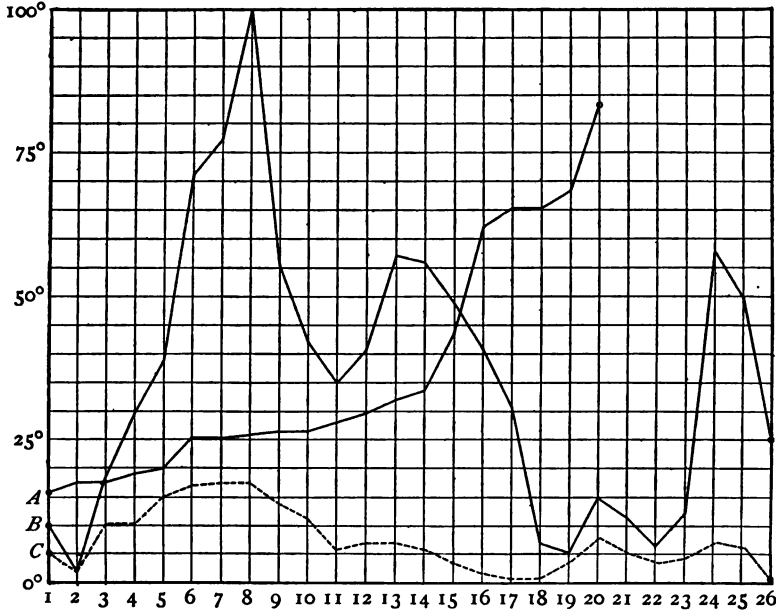


FIG. 46. Curves for sequence of genera and frequency of anatomical characters of the Cordaitales, Ginkgoales, and Coniferales: *A*, sequence of genera; *B*, specific characters; *C*, generic characters

conditions involved, the branching system of the Norway maple (*Acer platanoides*) seems best suited to an illustration of all these phases of terminal growth, suppression, and relations of successive members which we conceive to be represented in the development of plant phyla, inasmuch as it conveys the idea of succession through lateral members in such a way as to indicate the chief line of descent. The branch of the Norway maple, when of vigorous growth, is a monopodium, and it is obvious that such would

not answer the object in view, since its most prominent feature would suggest the idea of a continuous series of conterminous members, from which lateral members would arise at intervals. There is no evidence that any phylum represents such a series; on the contrary, there is every reason to believe that such relations do not exist among the various groups of plants.

In those branches of the Norway maple which exhibit slow growth various forms of arrested development are manifested. These take the form of atrophied buds, or of branches in all stages of development, and there thus arises a modified monopodium which eventually becomes, in many cases at least, a true sympodium. In comparing this with the monopodial branch of vigorous growth, it appears that the alterations involve more than mere suppression. In the monopodium the average angle of divergence for the lateral members is 45.3 degrees, while for the derived form it is 34.1 degrees. The latter will be seen to completely fulfil all conditions with respect to the development of a phylum, even to indicating the position of missing members. In the construction of this figure an attempt has been made to show all normally developed buds (O) and their relative dimensions; atrophied buds (o), the position of which is recognizable; and atrophied branches (Y) which are still visible, but it is obvious that the figure does not show many members all evidence of the former existence of which has completely disappeared. Selecting from this we obtain the accompanying figure, which embodies our final conclusions as to the general succession of the different gymnosperms, and from it we may gather that the highest representative, *Pinus*, is the terminal member in the main line of descent from the *Cycadofilices* through *Poroxylon*, while from such a central line both the *Cordaitales* and *Gingkoales* have been given off as side lines.

The general results of these investigations serve to confirm in a very striking manner the probable monophyletic origin of the gymnosperms, as already expressed by Coulter (11), while they also show that the real transition ground, at least for all but the *Cycadaceæ*, was probably represented by *Poroxylon*, as indicated by Scott (81).



## CHAPTER XII

### DURABILITY OF WOODS AND THEIR PRESERVATION AS FOSSILS

One of the most important questions which enters into the consideration of those who are called upon to employ timbers for the various constructive purposes to which they are adapted, is their ability to resist decay in its various forms, or their durability. Different species of woods vary widely in this respect, as may be readily ascertained by consulting the data collected by Professor C. S. Sargent in his Tenth Census Report upon the *Forest Resources of the United States*, and as appears in the second part of the present work. In general terms it is probably true that the more resinous woods are more durable than those which are less resinous, this being the direct result of the preservative action of the resinous material, which is in itself highly resistant to decay, and which further acts through its somewhat well-defined antiseptic properties and therefore behaves toward the general structure as a natural preservative, while it also excludes water from the interior parts and thus tends to limit the operations of fungi. Thus it may be stated broadly that the resinous conifers as a whole are more durable than the nonresinous woods of the higher angiosperms. Or among the conifers themselves the hard pines are more durable than the soft pines, as may be seen by a comparison of the southern pine (*Pinus palustris*) with the white pine (*Pinus strobus*). But apart from the presence of resin, which may be localized or distributed throughout the entire cellulose skeleton, it is altogether probable that the durability depends to a very large extent upon inherent properties of the cell membranes which have become variously modified in the course of growth and thus adapted to this end. Thus it has already appeared (Chapter III, p. 48) that while the unmodified

cellulose contains approximately 44 per cent of carbon, the lignified tissues contain upwards of 68 per cent of this element. From this we are led to conclude that tissues yield to or resist decay just in proportion to the extent of such modifications, which are to be regarded as of a protective character. If this principle be extended to lignified tissues in general, we must then admit that since the extent and quality of the lignification do not develop equally in all species, these latter must exhibit corresponding differences with respect to their ability to resist the disintegration attending what is commonly called decay, whether such decay arises primarily as a process of slow oxidation, or whether it is initiated through the operation of active enzymes. The general law thus stated has an illustration in a very striking instance of the relation which the special character of the cell wall bears to agents promotive of decay, as recorded by von Schrenk (68, 49), who shows that while *Polyporus versicolor* readily attacks the living catalpa tree and produces widespread decay, there is no fungus which will attack the timber when once it has been cut and seasoned, — a fact which serves to explain the astonishing durability of this wood in spite of its great porosity.

Another factor of great importance is to be found in the conditions which immediately surround a given timber, since it is a well-known fact that the same species of wood does not exhibit the same degree of durability under all conditions. Thus wood in a well-drained and well-aërated soil will have a much longer term of life than it would in a wet and badly aërated soil. Or, again, the same difference would hold true as between a comparatively sterile soil and one which is rich in organic compounds. The life of a timber in salt water is far greater than in fresh water, or even than in well-drained soil, owing to the specially preservative action of the salt; while the durability may be indefinitely prolonged if the wood be hermetically sealed in an impervious matrix such as clay. These differences are readily susceptible of an explanation by reference to the relation which the various media bear to the growth of fungi and bacteria, since we recognize in these two groups of plants the active agents



which constitute the source of decay. It is not our purpose to discuss the particular mode of action of these organisms at the present moment, since that is more appropriately reserved for a subsequent chapter, but a few concrete examples will serve to indicate somewhat more exactly the relative durability of certain species under widely different conditions.

One of the most instructive examples to which our attention has been drawn, not only because of the very perfect state of preservation but also because of the great length of time the wood has resisted the action of decay, is to be found in *Sequoia Penhallowii*, as recorded by Jeffrey (25). The wood in question, representing a large fragment of a tree at least six feet in diameter, presents the external aspects of a recently cut piece taken from an existing tree. It is of Miocene age, and was obtained from the Sierra Nevada Mountains on the line of the Central Pacific Railway, under sixty feet of conglomerate, where it was located in the auriferous gravels. No difficulty was experienced in making sections of this wood for the microscope, no more than would be encountered in wood taken from an existing tree, since it was very slightly silicified. A microscopic examination shows the structure to be most beautifully and perfectly preserved in all its details; while several beautifully prepared sections, for which I am indebted to the courtesy of Dr. Jeffrey, also make it evident, from the complete absence of fungus mycelia, that these latter had not found their way into the tissues at any time during the long burial of the tree. The special interest of this wood centers in the fact that, so far as I am aware, there is no other example of an uninfiltreated and unaltered wood from so ancient a formation.

More recent Tertiary strata afford numerous examples of a similar character. The Pleistocene in particular has furnished many instances of the most perfect conditions of preservation, chiefly of woods which, under ordinary circumstances, would be regarded as "durable." In 1898 Professor A. P. Coleman of Toronto obtained from the Pleistocene clays of the Don valley, at that place, a specimen of the common red cedar (*Juniperus virginiana*)

which exhibited all the external features of that species, including the characteristic color and fibrous bark (48, 562)\*. When cut with a saw the well-known odor was given off somewhat freely. Under the microscope the structure was found to exhibit no evidence of alteration, while there was seen to be only a limited development of mycelial filaments, — not as much as may often be found in badly seasoned logs. This condition of preservation is to be ascribed chiefly, no doubt, to the fact that the wood was hermetically sealed in an impervious clay which completely excluded all fungi and inhibited further growth of those originally present. This explanation appears the more probable from the fact that leaves of the *Vallisneria spiralis*, embedded in the same clays, show all the details of the original structure when freshly exposed, and it is only upon subsequent dessication that disorganization takes place.

*Juniperus californica* from the interglacial deposits of Humboldt County, California (46), offers a very similar though much more instructive example of preservation through long periods of time. This wood was obtained from two localities, in the one case occurring in blue, sandy silt under one hundred and fifty feet of local débris, while in the other case it was embedded in blue, slaty muck under fifty to sixty feet of local débris. A microscopic examination showed that the structure contains very few mycelial filaments, in fact only slightly more than in the Don specimen of *Juniperus virginiana*. The structure of the tissues is well preserved and gives no evidence of that obliteration of parts which usually accompanies the operation of fungi and bacteria, whence we may correctly infer that such organisms were not operative. It was nevertheless found that the tissues did not offer the normal amount of resistance to the action of the knife in cutting sections, the result being a localized fragmentation. The material was only very slightly silicified and there was no difficulty in the removal of the mineral matter, but the entire structure presented unusual thickening of the cell walls, such as would arise through the action of strong alkali. Alterations of this character are not infrequent among fossil plants, most

particularly among those which are eventually silicified, and in the present instance they serve to explain the mechanical weakness of the tissue, the cellulose substance of which has undergone a gradual molecular alteration consequent upon the action of an alkaline solution — possibly of a hot spring — which has been continued indefinitely.

The Douglas fir is regarded as one of the most durable of woods, and it is not surprising to find instances of its perfect preservation under very adverse circumstances. Specimens of *Pseudotsuga macrocarpa*, from the same beds as the Californian juniper already described, exhibit the same absence of special silicification, but they differ in a much more marked development of fungus mycelia, and in a somewhat extreme alteration through the action of free alkali, which has been carried so far that in the summer wood the cell cavities are largely obliterated, while the thinner-walled tissue of the spring wood shows definite collapse. Apart from this there is no evidence of the removal of parts through the action of decay, and we may conclude that the fungus present had not produced any specific effect. Yet another illustration is afforded by *Pseudotsuga Douglasii* from Mystic Lake at Bozeman, Montana, where it was found under eight feet of the old lake-bed deposit, which antedates a well-defined and superimposed glacial deposit. The age of this formation is open to discussion, as it may represent local glaciation of recent date, while there is also a possibility that it may be synchronous with the continental interglacial period, since the absence of the tree from the same locality at the present day leads us to suppose that its removal occurred in the time of general glaciation, as may be inferred from other evidence (46). In its external aspects the wood presents a remarkably perfect state of preservation, exhibiting all the features of grain and other structural details, even to an exhibition of the bordered pits, which may be readily determined with a hand lens of moderate power. Furthermore it was wholly free from infiltrated mineral matter and was readily softened in boiling water so that sections could be cut with the greatest ease. Internally the

structure was found to be most perfectly preserved in all its details, showing no evidences of decay and a remarkable freedom from fungus mycelia, from which we may conclude that the tree was not only buried but practically hermetically sealed up—possibly by the operation of an avalanche—before an opportunity for the action of fungi and the operations of decay was possible.

The genus *Picea* is a widely distributed type in the Pleistocene deposits, particularly in Canada. A large amount of material has been obtained from the Pleistocene clays of the Don valley at Toronto and elsewhere, and it affords an excellent index of the durability of the wood under such conditions. All of the material has been found to be devoid of silicification or other mineralization, and it presents somewhat diversified aspects with respect to conditions of preservation. *P. alba*, of the Scarborough period, although the wood is fairly well preserved as a whole and readily admits of a determination of the species, shows a great abundance of fungus mycelia. Wherever this is to be found there is a marked alteration in the structure of the cell wall, involving a breaking down of the secondary layer, as usually occurs under such circumstances, this disintegration being always most marked in those regions where the mycelium is most abundant. In this case the relation of the fungus to the changes noted is very obvious.

*Picea nigra* from the Don deposits is in some cases so well preserved as to permit of a determination of the species without difficulty, while in other cases the decay has progressed so far as to render identification impossible. Fungus mycelia are always present and they clearly constitute the active agents of decay. The widely different conditions of preservation here represented suggest the operation of specific causes wholly apart from the inherent qualities of durability which the wood naturally possesses. These are to be sought for in two directions,—either in local conditions of preservation, as varying permeability of the soil, or in the conditions of decay established prior to entombment. All of the material has been derived from

a compact clay, which offers a practically air-tight matrix of essentially the same physical character in all cases. It therefore seems improbable that local variations of the inclosing material could have been so different as to give rise to the diverse aspects of decay noted, though such may have been a factor of secondary importance. The fact that under essentially the same conditions some specimens were well preserved while others were badly decayed, at once directs attention to the probable operation of antecedent causes. It is quite obvious that trees which eventually become fossilized are neither of the same age when they fall nor are they in the same condition of soundness. Some may be quite sound, while others may be infested with fungi, and the living tree may therefore present the somewhat advanced progress of decay. But the fossils of the Don deposits are obviously fragments of trees which had been brought, through the agency of water, to the places where found, and it is quite clear that while some of the trees may have been speedily buried others were no doubt a long time in the water before being inclosed in the sedimentary deposits. Decay would have an opportunity for extended development under such conditions, and it would even continue for an indefinite period after entombment. On the other hand, the rapid entombment of a vigorous tree in which decay had not yet made its appearance might involve the inhibition of fungoid growth. On this hypothesis, which seems to present the preferable alternative, it is possible to satisfactorily account for the varied states of preservation noted, as arising under essentially uniform conditions.

The common larch (*Larix americana*) is another wood of very widespread occurrence throughout the Pleistocene deposits. Two widely separated localities may be selected as affording examples of its preservation. At Dahlonga, Georgia, this species has been found in the black clays, which are to be regarded as probably synchronous with and equivalent to the Pleistocene deposits of more northern localities (51). The material was found to be wholly free from impregnation with mineral matter, but it exhibited the somewhat extreme effects of advanced decay with the

subsequent operation of pressure,<sup>1</sup> so that it was with some difficulty that sections were made which would show structure. The entire structure showed abundant fungus mycelia, while the walls of the tracheids had suffered such reduction under the operation of decay that the secondary walls were largely removed with a corresponding obliteration of structural markings, and the whole fabric was reduced to a compressed and greatly modified skeleton consisting of the primary cell walls. Numerous specimens from the Don valley show that while some are full of fungus hyphæ and present a correspondingly advanced state of decay, others from precisely the same locality show a total absence of all fungoid growths and a completeness of structural details which leaves nothing to be desired by way of comparison with recently cut material. Here it is still more evident that the explanation applied to *Picea nigra* is not only applicable in this case also, but that it affords a correct insight into the reason for the various conditions of preservation of wood which, when embedded in clay, is practically imperishable. A more recent example of the larch may serve to lend emphasis to these conclusions, and it is of particular interest because it embodies the changes which may arise in the course of practical use. In the Peter Redpath Museum of McGill College there is a specimen of an old aqueduct log which was laid down in the early days of Montreal. The old and long-forgotten pipes were uncovered in the course of excavations for a new water main on St. Paul Street. They were about one foot in diameter, with a two-inch bore. According to a communication in one of the daily papers, the pipes were laid about eighty years previous, but were in use for only a short time. An examination showed that when the pipes were recovered they were practically sound, with the exception of the superficial layers, which had so far yielded to decay as to be in process of removal, and the external form had thereby suffered some alteration. A microscopic examination showed the structure to be so perfectly preserved as to admit of

<sup>1</sup> Recent studies indicate that the amount of pressure required to produce such results need not be very great, probably less than one hundred pounds.

identification without any question, and there was but slight evidence of the operation of decay, a fact which goes far to support the hypothesis already discussed, that if the wood is sound when buried in a compact and air-tight matrix, its decay depends essentially upon that which had been initiated before inclosure, and that otherwise there is essentially no change.

Upon assuming charge of the office of governor of Montreal in 1642, Maisonneuve constructed a palisaded fort near the present location of the customhouse. In 1890, in the course of excavations in that locality, the workmen uncovered hewn timbers which were held to represent a portion of the palisade of the old fort. A specimen of one of these may now be seen in the museum of the Natural History Society of Montreal. It represents the wood of the common red pine (*Pinus resinosa*). Externally the wood has all the aspects of a recently cut log, a state of preservation which is amply supported by microscopical examination, from which we learn that there is very little mycelium present, and that the structure is as perfect as if taken from a tree of present growth, notwithstanding its probable burial for two and one-half centuries.

Data of a more recent character with respect to the duration of timbers used for constructive purposes may be derived from actual experience. Thus Dudley has found that when the yellow pine (*Pinus palustris*) is employed in the ground or used as ties, it very quickly decays, being destroyed by the action of *Lentinus lepideus*, Fr., although the wood is very durable under conditions of comparative dryness (14). In the case of ties from the Panama railway, he also points out that they were useless in two years, while similar ties employed in the southern states lasted from four to six years, and in the middle states they lasted from five to eight years, showing very clearly the influence of varying climatic conditions, particularly with respect to the relative humidity and temperature. According to the same authority, cedar ties (*Cupressus thyoides*) will last from eight to ten years, even when not wholly sound at the time of laying, while hemlock ties (*Tsuga canadensis*) have a life of only four

years. The relation of special conditions of moisture is further exhibited in these cases in the fact that ties which were perfectly sound on the exposed sides are very often found to be in an advanced state of decay throughout the buried parts. Mutilation is an important factor in the introduction of decay, and Dudley has shown (14) that where spikes have been driven into the ties, and where the structure has thereby suffered mechanical alteration, decay finds an opportunity for speedy entrance into the interior tissues, which it rapidly permeates and destroys. This relation of cause and effect is in perfect harmony with what has long been known to occur in living trees where broken or badly amputated limbs afford an opportunity for fungi to penetrate and destroy otherwise healthy tissues.

The preceding considerations have directed attention to the fact that coniferous woods may be preserved indefinitely, provided they are completely excluded from fresh supplies of free oxygen and are maintained under conditions of low temperature,—in other words, hermetically sealed in an impervious medium. While we are thus in a position to understand the conditions under which a very large proportion of woods are preserved as fossils in the more recent geological strata, no explanation is offered which will adequately account for the mode of preservation of the large number of plants met with in the older rocks, even as far back as the Devonian and Silurian, and it is desirable that examples of these should be passed in review. In this connection four principal forms of preservation may be noted, — (1) carbonization, (2) silicification, (3) calcification, and (4) pyritization.

*Carbonization.* This form of preservation is essentially characteristic of plants derived from the coal measures, and it is represented by coal itself. It depends essentially upon a gradual withdrawal of the elements of water from the original cellulose substance, whereby a relative excess of carbon is developed. It is a change which takes place under exclusion of air, and it is no doubt facilitated by the action of heat and possibly also of pressure. It is obvious, however, from the nature of the changes



involved, that they not only proceed very slowly, but that it is possible to find plant remains which present different stages of the process, as represented by the various forms of peat, brown coal, soft coal, and anthracite. Being determined by the withdrawal of hydrogen and oxygen from the original tissues, these alterations must arise very unequally in different parts of the plant body, as determined by the character of the tissue involved and the relative percentage of carbon originally present in the cellulose substance. In the progress of such changes, gases constitute some of the most abundant and conspicuous end products. While under ordinary circumstances they may be liberated continuously, they may be stored under favorable conditions, to be liberated in great volume at a later period. Thus it has been shown, as the result of recent observations (88), that where plant remains accumulate in large quantities, sulphureted hydrogen together with the light carbureted and phosphureted hydrogen arise. The two latter, being subject to spontaneous combustion, take fire upon coming in contact with the air, and, setting fire to the associated sulphureted hydrogen, an extensive conflagration may result. Phenomena of this kind on a large scale rarely come within the observation of man, but that such have been observed affords abundant ground for the belief that many forest fires of obscure origin are to be accounted for in this way. Thus, once more comparing the percentage composition of the principal cellulose modifications, it is found that normal cellulose contains 44 per cent of carbon, lignin about 62 per cent, while cork contains upwards of 74 per cent. In accordance with this principle it will be found that wood tissue becomes carbonized sooner than the softer parts of the structure, which may already have disappeared through the operation of decay, or the highly carbonaceous cork tissue of the bark may be converted into a structureless mass of carbon, while yet the less carbonaceous wood tissue is preserved in all its details. It is thus possible, in a silicified wood, to recognize and define the general limits of the bark by the carbonized layer which oftentimes forms the outer portion of a fossil wood.

Carbonization necessarily involves a more or less profound obliteration of structural details. This is especially true in those cases in which an absence of infiltrated mineral matter has prevented a retention of the original structural details, and where pressure in conjunction with heat, as in hard coal, has produced a secondary effect. From this point of view it is true that a highly carbonized cortex rarely presents any structural details. Lignites and some of the softer coals not infrequently present well-defined structure, but the same cannot be expected of the hard coals, in which extreme alteration has been effected. In many cases, such as may be found in the Devonian and later formations, carbonization is joined to silicification or calcification and gives rise to resultant forms of preservation, which will be discussed more fully and with more propriety in the next chapter; but attention may be directed to the general fact that where carbonization operates by itself the fossil acquires an opacity which renders it very difficult to determine details, while the structure also becomes so friable as to make special methods of section cutting imperative.

*Silicification.* This is by far the most common form in which the stems of plants are preserved in the older rocks. It depends upon the slow infiltration of a solution of an alkaline silicate into the tissues, whereby the entire structure eventually becomes converted into a mass of silica, as in the trees of the petrified forests of Arizona, or as may be seen in some of the larger algæ, such as *Nematophycus* from the Devonian. According to the rate of infiltration, relatively to the operation of decay, all structural details may be observed. Under ordinary circumstances, however, such a method of preservation is one of the most advantageous for the purposes of scientific study, because of the transparency of the mass and the permanent form of the material.

*Calcification.* This form of mineralization is much less common than silicification, with which it may be combined. In some cases, however, calcite constitutes the entire mass of the infiltrated material, as in the case of *Osmundites skidegatis*

from the Cretaceous of the Queen Charlotte Islands, which, as shown on a former occasion (56), contains at least 70 per cent of calcium carbonate. The general effect of this form of preservation upon the structure is substantially the same as in silicification.

*Pyritization.* A still less common form of preservation is that which involves a replacement of the silica or calcite of the previous forms by crystalline sulphide of iron. This is a feature more or less common to fossils from the older formations, which always involves a complete obliteration of structural details, though in rare cases the more general features may be seen when viewed by reflected light. Plants presenting this form of preservation are among the least valuable for purposes of scientific study.

## CHAPTER XIII

### DECAY: ITS MODE OF ACTION AND EFFECTS

In discussing the operation of decay in the woody tissue of a stem, it will be desirable to have reference to (1) the nature of the active agents, (2) the conditions under which they flourish, (3) their mode of operation, and (4) their effects upon the structure and mode of preservation.

1. *The nature of the active agents.* Decay has its origin in the growth of certain plants of a low degree of organization, which, through their ability to seek food supplies either in living or dead organic bodies, produce such an unusual course of development as to effect an actual disorganization of the tissues, as expressed in decay. To understand fully the nature and mode of operation of these plants, it will be necessary to briefly pass in review their essential characteristics.

Among the lower forms of plants we recognize two somewhat nearly related groups, which present many features in common, both with respect to their influence upon the promotion of disease and decay and to their general habits of life, but which nevertheless differ very materially in their structure and the details of their life history. The first group embraces what are known as the Bacteria, — plants characterized by their unicellular structure, which rarely assumes a filamentous form, and by the fact that while they may and frequently do propagate through the medium of spores, they more commonly multiply by simple fission, in consequence of which they are designated the *fission fungi* or *Schizomycetes*. Their life history is very simple, and the incomplete cycle, which is wholly devoid of a sexual phase, is repeated at very frequent intervals, so that they multiply with enormous rapidity. The nutrition of the bacteria is derived by a process of direct absorption from the surrounding

medium without the development of specialized organs for that purpose. Owing to their minute size they are readily distributed by even slight currents of air, from which they eventually settle as constituents of dust. Their spores offer a remarkable degree of resistance to ordinary conditions, whereby they may survive a most adverse environment for prolonged periods, and again produce the vegetative form when favorable conditions are once more established. It will thus be observed that the growth and operation of such plants is not necessarily continuous, but that their action may be intermittent or periodic, as determined by the special circumstances under which they are placed. In any event, the characteristics noted favor, in an exceptionally high degree, the wide prevalence of the effects of which they are the immediate cause. It would be out of place here to enter upon a detailed discussion of these effects, and it will suffice to direct attention to the very general relation of these plants to the production of disease in both plants and animals, while their relation to the disorganization of organic tissues is exemplified in the various processes of maceration which constitute so essential a feature in many important industrial processes.

The second group of plants includes the Fungi, — plants distinguished by their somewhat higher degree of organization and the development of specialized organs. They are generally multicellular, and the plant body, or *mycelium*, is in the form of a septate, or nonseptate and branching, microscopic filament, which is capable of very rapid extension, and which may also bring about a vegetative propagation by simple subdivision. At certain stages of its growth, as also under special conditions of moisture and temperature, the mycelium gives rise to asexual reproductive bodies, or *spores*. Such spores are very minute, and are composed each of a single cell. They may or may not arise through the medium of a sexual process, the fungi exhibiting a great diversity in this respect, a discussion of which is unnecessary at this time. The spores are generally produced in vast numbers ; they are most readily distributed by the wind

or even by slight movements of the air; their extreme buoyancy keeps them afloat for prolonged periods, though they eventually settle as one of the ordinary constituents of dust; they offer a high degree of resistance to deleterious influences, and are thus capable of bridging over critical periods, at the end of which they may germinate with great freedom. It will thus be seen that through such spores it is possible for the fungi to develop wherever and whenever favorable conditions are met with. The life history of the fungi is usually much longer and more complex than that of the bacteria, and while the life cycle often involves both a sexual and an asexual phase, the former may not appear throughout a very much prolonged period of development, within which the plant may nevertheless extend with great rapidity and produce all the characteristic effects of its growth.

Both the bacteria and the fungi are characterized by the absence of a green pigment, or chlorophyll, and their consequent inability to produce carbon compounds from the carbon dioxide of the atmosphere as a source of energy. With the exception of a few of the bacteria, the energy of all these plants depends entirely upon the oxidation of carbon compounds previously formed and accumulated by some other organisms, primarily those which contain chlorophyll. It is therefore imperative that such compounds should be derived directly from the nutrient fluids of a living organism, or *host*, upon which the *parasite* feeds; or that it should be obtained as one of the products of a decay induced by the fungus or bacillus which thereby becomes a *saprophyte*. From the nature of their process of nutrition, saprophytes are generally found within the body upon which they act, and they are thus *endophytic*. This is particularly true of the bacteria. The more highly organized fungi may live chiefly upon the surface of the body (*epiphytic*), sending the branches of their mycelium (the *hyphæ*) into the interior parts, where they develop specialized feeding branches (*haustoria*), which arise wherever food supplies are to be met with. Or, again, endophytic forms may reach the surface only at certain

periods of development and under special conditions of environment, when they become recognizable without the aid of the microscope by reason of their characteristic fruiting structures.

It is further true that in these two groups of plants there is a more or less variable relation toward the source of food supply. This is expressed by the classification long since adopted by De Bary (83), and now generally used with slight modifications, who recognized :

1. True or *obligate* saprophytes : those which obtain their food supplies from the products of organic decay under all circumstances.
2. Partial or *facultative* saprophytes : those which usually complete the life cycle as true saprophytes, but which, under special circumstances, may more or less completely but temporarily become parasites.
3. True or *obligate* parasites : plants which invariably derive their nutrition directly from the nutritive materials of living organisms.
4. Partial or *facultative* parasites : those which, under special circumstances, may become saprophytes, though ordinarily completing the life cycle as true parasites.

Among the very large number of parasites and saprophytes which attack timber, either living or dead, it will be found that within certain limits there is a more or less well-defined relation to the organism affected, whereby it is characterized by the growth of special forms. The number of species peculiar to a given tree will be found to vary somewhat widely, and this will in turn be influenced within the limits of a particular species of tree by conditions of environment. Thus von Schrenk (68, 49) shows that the wood of *Catalpa speciosa* is injuriously affected by only two fungi, and the same is likewise true of the red cedar (*Juniperus virginiana*); but Dudley (14) points to the fact that no less than eighteen species of fungi infest the wood of the hemlock (*Tsuga canadensis*), of which nine are Polypori and six Agarics. Again, it is a well-known fact that other fungi, such as dry rot (*Merulius lachrymans*), are not selective in any particular sense, but by reason of their very cosmopolitan habits they grow within any wood, provided the external conditions of warmth and moisture are favorable. It by no means follows from the

above statement that all the fungi found in a particular wood either produce the same or even similar diseases, that they are equally active, or that they operate under all conditions; and it will suffice in this connection to again direct attention to the results obtained by von Schrenk in the case of the hardy Catalpa, with respect to which he shows that soft rot produced by *Polyporus versicolor* (L.), Fr., rapidly destroys the heartwood, while the brown rot induced by *Polyporus catalpæ*, von Schr., operates throughout the trunk near its base; and yet again, while these two diseases produce specific and distinct effects in the living tree (68), there is as yet no fungus known which will grow in the tissue of the catalpa wood after it has been cut and dried,—a fact which readily explains the remarkable durability of this wood and its adaptation to purposes where freedom from decay is a first consideration.

2. *Conditions under which they flourish.* In entering upon a discussion of the conditions under which fungi operate in plant tissues, we must assume, as is in reality true in all cases, that the latter contain an appreciable amount of material which may be utilized by the fungus for the purposes of its own nutrition. Such food material is always presented by the cellulose substance of the cell wall, which is thereby broken down and gradually removed, though this does not occur usually until other and more available forms of food material have been exhausted. In the second place, the nutrient material stored by the plant for its own sustenance, such as the starches and sugars, are readily attacked by fungi, and so long as they last the invading organism confines its operations chiefly to those regions and particular cells in which such storage is most marked. Apart from such conditions of food supply, which must be held to be of fundamental importance and to be a constant factor under all circumstances, air, temperature, and moisture must also be regarded as essential though variable factors which operate as the real determinants in the growth of the invading organism.

The active growth of all plants demands an abundant supply of oxygen. In the vast majority of cases this gas is derived



directly from the air, or indirectly through the medium of the surrounding fluid, such as water, in which the organism may be growing. Such aërobes cannot exist when the supply of oxygen from either of the sources indicated is cut off, since their respiratory function is inhibited and all dependent activities necessarily cease. It is true that some plants, such as certain of the bacteria, cannot live under such conditions of free aëration, inasmuch as they have become adapted to obtaining their oxygen from the products of organic decomposition, and any access of air or free oxygen at once inhibits their growth. Such anaërobes form a comparatively small but none the less exceedingly important group of plants, and it is a knowledge of these differences in the life history of the organism which enables us to gain an intelligent insight into the operation of the various forms of organic decay. It may be stated, then, that the fungi in general cannot grow except under conditions which afford a free supply of oxygen, and this fact supplies the basic principle on which to found methods for retarding or permanently arresting the operation of fungi. But it will be found in practice that this is further dependent upon the remaining factors of warmth and moisture. In the preceding chapter it has been shown that the spores of fungi, as also those of the bacteria, are capable of entering upon a resting state whereby they become capable of resisting very adverse influences, but that they are also capable of once more germinating, sometimes after the lapse of several years, when again brought under favorable conditions. These conditions are (1) a suitable temperature, and (2) an abundance of moisture. The consideration of a few special cases will permit of a clearer conception of the nature and operation of these conditions.

That all fungi are not equally affected by the same degree of heat and cold is one of the elementary facts of plant physiology, while it is also equally well known that the same plant will be variously affected according to the special condition of growth in which it is brought under the action of varying temperatures. These facts are probably illustrated among the bacteria in a

more prominent way than in any other group of plants, though the general relations also hold true for all the higher fungi. Thus among the bacteria certain forms have been known to survive a temperature of  $-10^{\circ}\text{C.}$ , or even  $-100^{\circ}\text{C.}$  when the cold is applied for a short time only. On the other hand, *Bacillus thermophilus* thrives vigorously at a temperature of  $70^{\circ}\text{C.}$ , while the spores of the common hay bacillus (*B. subtilis*), which are destroyed when heated in their nutrient solutions to temperatures exceeding  $100^{\circ}\text{C.}$ , are nevertheless capable of resisting upwards of  $120^{\circ}\text{C.}$  of dry heat. From these and similar well-known examples it may be concluded that the specific effect of varying temperatures is due to the amount of water present in the albuminoid protoplasm, — a conclusion in accord with the reduction of water which is known to take place in a cell when it passes from the active vegetative to the resting state, in which form it manifests its highest powers of resistance to extreme conditions of temperature. This principle finds its further illustration in the fact that the vegetative cells of fungi, which contain a maximum of water and are adjusted to certain conditions of temperature, may be readily killed by dryness, for which purpose desiccation at the ordinary temperature is often sufficient. Broadly speaking, the bacteria cannot survive a temperature exceeding  $50^{\circ}$  to  $60^{\circ}\text{C.}$ , and in this connection a statement of the three critical points in temperature for a few well-known forms, as given by Warming, may be instructive :

	MINIMUM	OPTIMUM	MAXIMUM
Hay bacillus ( <i>B. subtilis</i> ) . . . . .	$6^{\circ}$	$30^{\circ}$	$50^{\circ}$
Anthrax bacillus ( <i>B. anthracis</i> ) . . . . .	15	20–25	43
Cholera bacillus ( <i>Spirillum cholerae-asiaticæ</i> )	8	37	40
Tubercle bacillus ( <i>B. tuberculosis</i> ) . . . . .	28	37–38	42

Turning our attention to the fungi, which are more immediately concerned in the destruction of timber, we find that with the exception of certain specialized forms the three critical points in temperature may be stated as minimum,  $1^{\circ}$  to  $2^{\circ}\text{C.}$  ; optimum,

20° C. ; maximum, 40° C. The relation of moisture and heat to continued life conforms to the same principle as stated for the bacilli, namely, that the spores of *Penicillium glaucum* and *Rhizopus nigricans* rarely germinate if exposed for one or two hours to air which has been heated to a temperature of 70° to 80° C., while they are entirely destroyed at 82° to 84° C. On the other hand, spores which have been heated in their own nutrient fluids to a temperature of 54° or 55° C. completely lose all power of germination (84, 725).

Although but little is as yet known respecting the life history of the fungi, and especially the particular conditions under which the germination of the spores occurs, the foregoing facts direct attention to the great diversity and wide range of the conditions involved for different species. Fortunately the researches of Hartig have made it possible to gain an insight of a more exact character into the operations of one of the most destructive fungi known, the dry rot (*Merulius lachrymans*), a short account of which may serve as a working basis for all fungi.

The spores of dry rot germinate on the surface of damp timber, and the growing plant quickly penetrates the tissue ; but the germination of the spores demands certain conditions which are fulfilled by the presence of alkaline products, particularly those which are ammoniacal. It will therefore be found that locations where there is bad drainage, especially in cellars and stables where ammoniacal products are likely to be abundant, offer exceptionally favorable situations for its development. When the plant has once entered upon its course of growth its extension is very rapid, and it thrives wherever the air is confined, warm, and damp, though it is well known that air, i.e. air which is freely circulating and which contains a much lower percentage of moisture, will cause the death of the plant in one or two days, except in deeply seated parts. From this point of view it may be observed that the disease is readily propagated in badly ventilated cellars or in confined areas where air does not freely circulate and there is a tendency to the collection of moisture. Thus in the construction of the MacDonald

Engineering Building at McGill University use was made of very fine timbers of Douglas fir as supporting beams to carry the heavy floors of the upper stories. These were seated in cast-iron, flanged bed plates. Within a few years, in the room used as a hydraulic laboratory, the timbers had developed dry rot, which extended upwards from the base for a distance of about one foot. The obvious cause was to be found in the confined air and in the accumulation of moisture condensed from the atmosphere of the room. In another case brought to my notice the heavy oak roof timbers of a large building developed an extensive growth of dry rot. Upon examination it was found that the air of the low attic was confined and no circulation was possible. Openings were at once made at opposite ends and a free circulation established. The difficulty was speedily removed, and there has been no recurrence of the trouble within a period of about fifteen years.

Our knowledge of the way in which and the conditions under which dry rot operates makes it possible to apply effective remedial measures with intelligence. These measures involve :

1. Complete ventilation.
2. Removal of all sources of alkaline and particularly of ammoniacal products.
3. A complete removal of all diseased wood.
4. Treatment with some fungicide, such as cupric sulphate, if the conditions are such as to make other remedies in any way ineffective.

Finally, the observations of Dudley (14, 44), that fungi do not penetrate cedar ties unless there is a good supply of air, and that when the latter is cut off the growth stops, once more direct attention to the nature of the effective preventive measures.

From these considerations it becomes obvious that for fungi in general higher temperatures offer correspondingly more favorable conditions for growth, which is also accelerated by an increase of moisture, both operating within certain well-defined limits. And we may further conclude that preventive measures will be most effective under those conditions which involve low

temperature, an absence of moisture, and, if possible, a complete exclusion of oxygen.

3. *Their mode of operation.* The mycelium, or plant body, of the fungus consists of a very slender thread which is about  $7\ \mu$  or less in diameter. Comparing this with the normal physical openings in the tissue of coniferous woods, it is found to be only one fourth the size of the cavity of the tracheid ( $28\ \mu$ ) of the spring wood, while it is but little smaller than the average tracheid cavity of the inner summer wood ( $10\ \mu$ ), and twice as large as the cavities of the tracheids last formed ( $3.5\ \mu$ ) in the wood of *Juniperus virginiana*. Within this same species it is but little smaller than the tangential diameter of the ray cell ( $8.7\ \mu$ ), while it is about twice as large as the average pore of the bordered pit ( $3.5\ \mu$ ). Red cedar was selected for comparison for the reason that the structural features referred to are relatively small and they represent what is common to a number of species, such as those of *Torreya* and *Taxus*. But it must be remembered that in the majority of coniferous woods the openings referred to are far larger, and they would therefore offer correspondingly more favorable conditions for free development of the mycelium. From these facts it is not difficult to perceive that when spores germinate on the surface of a timber, on a wounded surface, or in a crack, the growing plant at once finds ready access to the interior parts through the natural channels afforded by relatively large openings in the tissue. Such entrance will be greatly facilitated in proportion as the surface is rougher or the tissue is in any way lacerated, since such laceration not only increases the size and number of the initial openings but is also a factor which contributes to more speedy disorganization of the organic substance of the cell wall. From this it is evident that the stumps of branches which have been left in a ragged condition either through wind pruning or through the careless operations of the forester must afford conditions highly favorable to the operation of decay. Or yet again, when felled timber cracks in the process of drying before it is rafted, the cracks offer inviting places for the lodgment of fungus spores, especially

those of the *Polypori*, which abound in the forests. The subsequent immersion of the logs as they are floated to the mill causes the cracks to close and favors the development of the spores in the interior of the log. The relatively small amount of fungus developed under such circumstances lies dormant and is widely distributed wherever the prepared lumber is used for constructive purposes. If such boards should be employed in damp and close situations, such as a cellar or poorly ventilated basement, the fungus will find most congenial conditions for renewed and vigorous growth, and all the characteristic phenomena of dry rot will be manifested. An instance of this kind came under my observation some two years since in a city house, where the wainscoting of the basement dining room was once removed; but as the fungus again appeared within a short time and attacked the entire sheathing, the tenants sought safety in removal to another and better constructed house. A second case of the same sort was brought to a conclusion during the past summer. As a precautionary measure, about a year ago the infected woodwork was all removed and the surrounding walls were cleaned as thoroughly as possible, the surfaces being washed with a solution of cupric sulphate. Eventually, it being found impossible to check the trouble without much more extensive repairs than the landlord was willing to make, the tenant brought suit and secured damages.

When the fungus has once been established through any of the means described, and the conditions continue favorable, it extends with great rapidity in all directions from the original center, being guided in the course it takes by conditions of nutrition rather than the path of least resistance, carrying with it all the characteristic features of disease and decomposition. Wherever there is room for expansion, as in seasoning cracks or in the cavities arising through its own operations, the mycelium increases greatly and gives rise to massive developments of various forms. Thus in the white rot of the red cedar, caused by *Polyporus juniperinus*, von Schrenk has shown that the cavities arising through the action of the fungus are lined with a felt

of soft brown mycelium, which often assumes very fantastic shapes (69, 10).

In the diffusion of a fungus through woody tissue two important features may be noted: (1) the extent and direction of development are determined in the first instance by the distribution of food materials; (2) the distribution and progress of the mycelium are independent of the presence of physical openings in the structure. A few specific illustrations may serve to make these statements clear. No matter what particular channels may have permitted the mycelium to gain access to the interior, its development appears to arise chiefly and first of all in the medullary rays. The mycelium extends in the general direction of the ray structure and therefore at right angles to the principal lines of structure for the wood as a whole, filling the individual cells with loosely felted masses of brown hyphæ, from which are developed short and variously divided branches. These latter are particularly connected with the absorption of food substances, and they are appropriately known as *haustoria*. It very frequently happens that such growths of mycelium may be nearly or altogether confined to the structure of the ray, the adjacent tracheids being wholly devoid of them; or there may be local areas within which the mycelia extend vertically upward and downward from the ray, invading the neighboring tracheids, through which they extend for long distances. These facts suggest that the medullary ray may offer more favorable conditions for development than other parts of the structure, and they make it desirable to examine its structural features somewhat more closely from this point of view.

An examination of a medullary ray as exposed in radial section shows that the upper, lower, and side walls—particularly the latter—are provided with definite pits, through which it would be possible for the fungus to pass into adjacent cells with very little opposition. But such favorable conditions are obviously not taken advantage of to any great extent, since neighboring tracheids often remain quite free from the mycelium while the ray cells are crowded with it. This would seem to

imply that there is some special property in the ray itself which favors a more vigorous growth there, and serves to retain the fungus in that particular locality. The terminal walls, as in *Abies*, *Larix*, *Picea*, etc., are perforated with numerous pits, which would offer a somewhat easy path for the radial extension of the fungus. But such openings fail to satisfy the conditions and explain the great abundance of mycelium found in the rays, since the terminal walls of the *Cupressineæ* are not pitted but present a blank wall to the further progress of the fungus. Furthermore it may be shown, as will appear very shortly, that physical openings offer no determining influence upon the direction of growth of the mycelium, which continues in the originally selected course without respect to the structural characteristics of that which may lie in its path. From these facts, then, it would seem that the structure of the ray does not afford an adequate explanation of the observed phenomena.

The medullary ray constitutes perhaps the most important structural region within the vascular cylinder with respect to the accumulation of reserve food. This is deposited in the form of starch and other easily assimilated products, and it is their presence in relative excess which undoubtedly determines the abundant development and localization of the mycelia within such regions in the first instance. If this hypothesis be regarded as a correct one, then it is possible to see how the mycelia gain access to other structures exactly in accordance with its requirements and the possibilities of finding fresh stores of food material, which may be held to appear in diminishing quantities as successive areas are entered, until, the more available forms of food having been exhausted, the cellulose fabric itself is attacked, and with its disintegration the characteristic features in the operation of the fungus are expressed in recognizable form. In confirmation of the view thus expressed, it will be found to be very generally true that next to the medullary ray the greatest development of the mycelium takes place in the tracheids and resin passages, which they traverse in a longitudinal direction (plate 9). In this case it is possible that the opportunities for



free growth afforded by the long cavity of the tracheid or resin passage may serve somewhat to influence the direction of growth as the fungus searches for food, although, as in the previous case, it cannot be regarded as a determining factor of primary importance, inasmuch as there is a constant tendency to the formation of branches which traverse the wood at right angles to the walls. The third phase in distribution is established when the vertical strands give rise to hyphæ, which are developed at right angles to the original course, and which then traverse the tissue at right angles to the principal lines of structure (plate 10).

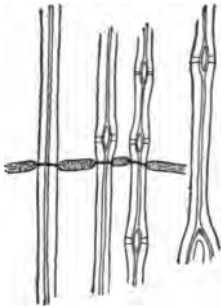


FIG. 48. *PINUS RESINOSA*. Radial section showing the progress of a fungus mycelium across the line of structure, and its penetration of the cell wall, independently of the presence of pits.  $\times 350$

It might be supposed that the course of the fungus would be determined by the presence of physical openings in the walls of the tracheids, and that the mycelium would therefore follow an irregular course leading it through the various bordered pits, which, as previously shown, offer ample opportunities for such passage. Such, however, is in no sense the case. In fig. 48 a radial section of the red pine (*Pinus resinosa*) shows very clearly that the growth of the fungus is wholly independent of physical openings of any kind, otherwise it would take advantage of

those which lie in its immediate neighborhood. On the contrary, its course does not deviate from the original direction established at the point of emergence from the main filament. Whenever in its progress the mycelium comes in contact with the cell wall, its enzyme attacks the latter, and by solution establishes an opening through which the fungus passes. It will be noted, nevertheless, that the resistance offered by the wall is sufficient to bring about a great reduction of the mycelium, which is always much less than the normal diameter within the limits of the wall. In thin-walled cells, where little resistance is offered, the opening thus established is commonly larger than the mycelium,

which then has a perfectly free passage; but in all highly lignified tissues, and more particularly those in which secondary growth of the wall is excessive, such contraction is always exhibited. This action of the mycelium in perforating the cellulose wall is by no means exceptional or peculiar to the fungi, since it appears in a variety of forms throughout the plant world and constitutes a well-known process in the liberation of spores from the mother cell, as well as in the progress of the pollen tube through the structure of the style.

It now remains to inquire somewhat more particularly into the specific action of fungi as expressed in

4. *Their effects upon the structure and their relation to forms of preservation in fossil plants.* While the general course of the physical changes in decaying wood is fairly well known, there are many features which demand more thorough and extended study. This is particularly true of the changes which arise in the cellulose and eventually resolve it into its proximate elements, whereby the chemistry of decay is recognized as one of the most obscure problems with which the plant physiologist has to deal. Nevertheless reference to the well-known reactions for cellulose, as already given (p. 49), enables us to form some conception of the nature of these changes, since those which proceed from the action of fungi are in many respects parallel with those obtained through the action of reagents. The alterations accomplished by the latter, either through the action of an acid or of an oxidizing body, are brought about in the fungi by the action of special ferment secretions included under the general name of enzymes. But here it is to be noted that each fungus behaves in a way peculiar to itself, and gives rise to specific effects which cannot be associated with other fungi. These differences may be reduced in the first instance to two groups, in the first of which the action is primarily upon the intercellular substance, whereby the latter is destroyed with a separation of the secondary walls from one another; in the second place the action is upon the secondary walls, which are largely removed with the production of a skeleton composed of the primary

walls. The specific action in such cases is probably one of hydrolysis, whereby the cellulose is resolved into soluble products of the general nature of glucose, and the results are precisely parallel with those produced by Mangin's maceration or by strong sulphuric acid. But such changes should be studied through the records of special cases. Tubeuf (72, 38-39) has shown that *Trametes pini* acts in the first instance upon the more highly lignified portions of the wall. The first effects of its operations, therefore, are expressed in the solution and removal of the primary wall, while the secondary and tertiary walls remain behind as a skeleton, which may eventually become corroded and disappear after prolonged action.

Precisely the same action has been reported more recently by von Schrenk as developed in the white rot of the red cedar through the action of *Polyporus juniperinus*, von Schr. (69, 9-10). The holes produced in the trunk of the tree through the action of this fungus often contain as much as three hundred grams of the cellulose fiber. On the other hand, the same author shows that in the red or brown rot of the same tree numerous pockets are formed in the wood. These are occupied by metamorphosed wood tissue which has cracked by shrinkage so as to form small cubes adhering to the walls of the pockets. An examination of such brown material shows it to be the residue of the original structure after elimination of the cellulose, the action involving a reduction of the cell wall by solution of the less lignified parts, thus reducing the original structure to the primary cell wall. Here again the action is seen to be exactly contrary to that of the previous case, since, while in the white rot the soluble substance, or hadromal of Czapek, is all removed, leaving the cellulose behind, in the brown rot the cellulose is removed, leaving behind a residue which von Schrenk has been able to identify with the so-called hadromal.

By the same authority identical changes have also been shown to arise from the action of *Polyporus versicolor* in producing the soft rot of *Catalpa speciosa* (68, 50-52). Tubeuf has also directed attention to the fact that the same general changes may

arise in other conifers through the action of *Polyporus vaporarius*, *P. Schweinitzii*, and *P. sulphureus*, one of their characteristic results being expressed in a breaking up of the cell wall into a series of spiral fibers corresponding to the original striation. This feature of decay is very commonly expressed in macerated woods among existing species, and it is exemplified in a very striking manner by *Pseudotsuga miocena* from the Miocene of Oregon (plate 11).

Whatever particular form the decay effected by fungi may take, it is no doubt correct to say that the disorganization of the cellulose is due in general terms, and in the first instance at least, to a process of hydrolysis. From this point of view it is possible to satisfactorily explain the varying degrees of resistance offered by tissues of different degrees of modification, since it will be observed that the decay acts inversely as the amount of carbon present, wherefore the unmodified walls are the first to be acted upon, the cork and cutin the last.

The changes thus noted as arising through the action of fungi have a more or less profound effect upon the degree of perfection with which structural details are retained when the plant eventually becomes silicified or calcified and is converted into the condition of a fossil. It has been shown that even when present in the tissue, the destructive effects of the fungus may be inhibited by the exclusion of oxygen, with the result that the structure is preserved in a most perfect manner through indefinite periods of time, and without the subsequent infiltration of mineral matter. Most commonly the wood exhibits the effects of more or less extended decay, which, in the majority of cases, shows a removal of the secondary wall and the formation of a thin-walled skeleton, which readily collapses and thus gives rise to extended distortion of the whole structure, whereby it becomes exceedingly difficult to recognize even the genus. If these changes proceed simultaneously with the infiltration of mineral matter, the latter may eventually replace the former to such an extent that while the lines of structure are preserved, they are but faintly defined by thin lines of finely granulated

matter representing the carbon residue of the original structure. Such a condition is presented in various species of Cupressoxylon and Pityoxylon from the Permian and Cretaceous of Kansas (45, 76-77). Eventually, as so commonly expressed in specimens from the petrified forests of Arizona, the silica may entirely replace the organic matter with an absolute obliteration of all structural details. Such alterations are necessarily regional and local, as determined by the more or less energetic action of the fungus and the progress of infiltration, of which two factors it is the necessary resultant.

A peculiar combination of decay and infiltration may, under other circumstances, give rise to a false structure which bears no relation whatever to the normal. This has been recognized by Penhallow on former occasions (57, 117, and 58, 25) in the case of the so-called Celluloxylon primævum of Dawson, which he has shown to be nothing more than peculiarly altered forms of Nematophycus Logani and N. crassus. No similar instance has yet been recorded for the vascular plants, and it would almost seem as if the alterations noted were to be specially identified with the more resistant forms of marine algæ. The peculiar changes observed in these plants were of such a nature as to give rise to tissuelike figures, which, under a low power, present the precise aspects of a coarse parenchyma tissue in process of decay. Such appearances led the late Sir William Dawson to recognize in Celluloxylon primævum a distinct type of plant, though it was subsequently shown that the appearances were wholly due to highly altered forms of Nematophycus. The effect arises from the fact that the carbon residue, the decay of which has already been carried to an extreme point, is in a finely granulated form, which admits of very ready redistribution. The crystallization of the infiltrated silica at such a time supplies exactly the necessary conditions for such redistribution. Under these circumstances the carbon particles arrange themselves upon the surfaces of the crystals without any reference to the original lines of structure, but in such a way as to produce definite figures of the size of the silicious crystals.

**NORTH AMERICAN GYMNOSPERMS**

**PART II—SYSTEMATIC**

#### NOTE

Genera and species which are also represented in the fossil state are indicated by \*.

Genera and species which are exclusively found in the fossil state are indicated by \*\*.

## PART II—SYSTEMATIC

### SYNOPSIS OF GENERA FOR THE CORDAITALES, GINGKOALES, AND CONIFERALES

#### A. Resin passages and fusiform rays present.

- I. Fusiform rays narrow, the terminals chiefly long and abruptly linear; the cells rather small and thick-walled. Resin passages with thick-walled epithelium and chiefly without thyloses.

Tracheids (radial) with spirals, at least in the spring wood.

Resin cells scattering on the outer face of the summer wood.

18. *Pseudotsuga* (p. 271).

Tracheids wholly without spirals.

Pits on the tangential walls of the summer tracheids.

Resin cells present but scattering on the outer face of the summer wood.

19. *Larix* (p. 276).

Resin cells wholly wanting.

20. *Picea* (p. 281).

- II. Fusiform rays (tangential) chiefly broad, the cells large, the resin passages broad with thin-walled epithelium and strongly developed thyloses.

Tracheids wholly without spirals.

Resin cells wholly wanting.

Pits on the tangential walls of the summer tracheids.

Ray tracheids not dentate.

21. *Pinus* (Section I, p. 305).

Pits on the tangential walls of the summer tracheids usually wanting.

Ray tracheids dentate.

21. *Pinus* (Section II, p. 318).

- III. Fusiform rays (tangential) wholly wanting. Resin passages (transverse) when present usually in compact rows on the outer face of the summer wood of distant growth rings, imperfectly formed.

Resin cells prominent.

Pits on the lateral walls of the ray cells usually with a conspicuous border, the orifice very large, oblong, the pits very prominent.

13. *Sequoia sempervirens* (p. 224).

Pits on the lateral walls of the ray cells very small, with a narrowly oblong orifice. Terminal walls of the ray cells strongly pitted.

17. *Tsuga Mertensiana* (p. 270).

Resin cells remote and more or less obscure on the outer face of the summer wood or wholly wanting.



Pits on the lateral walls of the ray cells small, simple, elliptical.  
Terminal walls of the ray cells more or less strongly pitted.

16. *Abies* (p. 253).

*B.* Resin passages and fusiform rays wholly wanting.

I. Tracheids (radial or tangential) bearing thin spiral bands in 1-4 series.

Ray cells (tangential) narrowly oblong.

Tracheids (transverse) chiefly thick-walled and variable, the lumens usually conspicuously rounded, the structure somewhat compact (except *T. floridana*), the spirals rather close.

6. *Taxus* (p. 212).

Ray cells (tangential) broad, oval, or oblong.

Tracheids (transverse) large, chiefly squarish, and rather thin-walled, the structure rather open throughout, the spirals rather open.

5. *Torreya* (p. 210).

II. Tracheids (radial or tangential) wholly devoid of spirals.

1. Wood nonresinous, commonly bearing idioblasts with sphere crystals; the tracheids of 2 kinds (transverse).

4. *Ginkgo* (p. 209).

2. Wood resinous, devoid of crystal-bearing idioblasts; the tracheids (transverse) all of 1 kind.

Resin cells (transverse) prominent and in more or less conspicuous, tangential bands, sometimes of distant growth rings or again widely scattering.

Terminal walls of the ray cells entire, straight, more rarely curved.

Pits on the lateral walls of the ray cells large, with a distinct border.

Resin cells distinctly zonate.

Pits on the lateral walls of the ray cells round, the narrowly oblong orifice distinctly diagonal, the border very prominent.

10. *Taxodium* (p. 217).

Resin cells scattering.

Pits on the lateral walls of the ray cells oval, the oblong or lenticular orifice usually parallel with the cell axis, the border often narrow, sometimes obscure.

13. *Sequoia* (p. 223).

Terminal walls of the ray cells sparingly pitted.

Pits on the lateral walls of the ray cells wholly simple or with an inconspicuous border, chiefly small.

Rays (tangential) broad, very sparingly resinous, often 2-seriate at least in part.

11. *Libocedrus* (p. 219).

Pits on the lateral walls of the ray cells distinctly bordered.

Rays (tangential) usually rather narrow, more or less strongly resinous, 1-seriate.

15. *Juniperus* (p. 244).

Terminal walls of the ray cells entire or locally thickened, usually much curved, sometimes straight.

Resin cells (transverse) rarely in bands, chiefly widely scattering, sometimes wanting.

Ray cells (tangential) narrowly oblong.

12. *Thuja* (p. 220).

Ray cells (tangential) rather broad, the cells round, oval or transversely oval, rarely oblong.

Summer wood usually thin and of open structure.

Pits on the tangential walls of the summer tracheids usually large and open, prominent.

Rays (tangential) not *very* numerous.

14. *Cupressus* (p. 228).

Rays (tangential) *very* numerous.

9. *Podocarpus* (p. 216).

Pits on the tangential walls of the summer tracheids very flat and not very prominent.

7. *Thujopsis* (p. 215).

Summer wood dense, the spring wood open, thin-walled.

8. *Cryptomeria* (p. 216).

Terminal walls of the ray cells thick, more or less coarsely pitted.

Resin cells (transverse) not very prominent, remote, and more or less obscure on the outer face of the summer wood, sometimes wholly wanting (*Abies*).

Rays (radial) without tracheids (rarely present in *A. balsamea*).

16. *Abies* (p. 253).

Resin cells (transverse) rather prominent, more or less numerous on the outer face of the summer wood, rarely zonate.

Rays (radial) with conspicuous tracheids.

17. *Tsuga* (p. 265).

Resin cells (transverse) entirely wanting, being sometimes replaced by resinous tracheids which are chiefly located along the medullary rays, or sometimes scattering.

Bordered pits multiseriate, hexagonal.

Resin when present contained in tracheids (transverse) and forming plates (radial) simulating Sanio's bands, or opposite rays (tangential).

Growth rings not determinable.

Tracheids (transverse) chiefly equal and in very regular radial rows.

1. *Cordaitea* (p. 198).

Tracheids (transverse) very unequal and in irregular, radial rows.

3. *Araucaria* (p. 203).

Growth rings obvious, but poorly defined.

2. *Dammara* (p. 203).

Bordered pits in 1 row.

Resin when present contained in tracheids (transverse) and forming plates (radial) simulating Sanio's bands, or opposite rays (tangential).

Growth rings not very well developed.

3. *Araucaria Bidwillii* (p. 205).

Resin when present massive (radial), not in plates.

Growth rings very prominent and well defined.

16. *Abies* (p. 253).

## I. CORDAITALES

Growth rings rarely well defined. Wood more or less resinous, but devoid of specialized resin cells or resin reservoirs. Medullary rays all of one kind. Bordered pits on the radial walls of the tracheids, hexagonal and multiseriate.

## 1. \*\* CORDAITES, UNGER. PLATES 12 AND 13

*Transverse.* Pith of the Sternbergia type, the cells large, thin-walled, often resinous. Growth rings, when present, obscure, rarely somewhat conspicuous. Specialized resin cells and canals wholly wanting except in the bark, where they take the form of tubular, branching canals without epithelium, extending in the general direction of the stem-axis. Tracheids in regular, radial rows, conspicuously squarish, and often resin bearing.

*Radial.* Elements of the protoxylem spiral and scalariform, and often showing a graduated transition into tracheids with bordered pits. Tracheids with hexagonal, bordered pits throughout, on their radial walls only, in 1-5 rows. Ray cells usually of one kind only; the upper and lower walls thin and not pitted; the terminal walls thin, not pitted, generally curved; the lateral walls with bordered pits.

*Tangential.* Medullary rays rather numerous, 1-seriate or often 2-seriate in part.

This genus is wholly extinct and occurs only in Paleozoic strata. For a more detailed account of the thirteen known North American species, see Penhallow, *North American Species of Dadoxylon*, Trans. R. S. C., VI, iv, 51-97, 1901.

## SYNOPSIS OF SPECIES

The following synopsis is given provisionally as an aid to identification of the various species, without implying the absolute value of the differential characters.

I. *Growth rings present*1. *C. pennsylvanicum.*II. *Growth rings obscure or obsolete*

## A. Ray elements of two kinds, tracheids and parenchyma

Bordered pits in 2-3, rarely 4, rows.

Ray cells (tangential) oval or oblong, often narrow.

2. *C. Clarkei.*

## B. Ray elements of one kind only

Bordered pits in groups of 6-13.

Pits on the lateral walls of the ray cells 3-6, chiefly 4, per tracheid.

3. *C. Newberryi.*

Bordered pits in one row, compressed.

Ray cells (tangential) broad, round, or squarish.

4. *C. recentium*.

Bordered pits in 1-3, chiefly 2, rows.

Ray cells (tangential) broadly oval.

Ray cells about 31-57  $\mu$  broad.

5. *C. hamiltonense*.

Ray cells about 28-37  $\mu$  broad.

Pits on the lateral walls of the ray cells about 1-4 per tracheid.

6. *C. illinoense*.

Ray cells (tangential) oval or round.

Pits on the lateral walls of the ray cells 1-8, chiefly 2-3, per tracheid.

7. *C. materioide*.

Ray cells not determinable.

8. *C. annulatum*.

Bordered pits in 2-5 rows.

Ray cells (tangential) oval or oblong.

Pits on the lateral walls of the ray cells 2-4, chiefly 4, per tracheid.

9. *C. ouangondianum*.

Pits on the lateral walls of the ray cells 4-10, chiefly 6, per tracheid.

10. *C. acadianum*.

Ray cells (tangential) broad or squarish.

Pits on the lateral walls of the ray cells 2 per tracheid.

11. *C. ohioense*.

Ray cells (tangential) oval or round.

Pits on the lateral walls of the ray cells 1-5, chiefly 1-2, per tracheid.

12. *C. materiarium*.

Bordered pits in 5 rows.

13. *C. Hallii*.

### 1. *C. pennsylvanicum*, Dn.

*Transverse*. Tracheids 44 x 44  $\mu$  broad, the walls 6.7  $\mu$  thick. Growth rings present, the summer wood about 8 tracheids thick, the tracheids about 12.5  $\mu$  radially, the walls 3.1  $\mu$  thick. Resin passages and resin cells wanting.

*Radial*. Ray cells all of one kind, conspicuously but gradually narrower toward the ends, equal to about 3 tracheids; the lateral walls with round or oval pits, about 2-3 per tracheid.

*Tangential*. Rays medium, broad, the cells round or transversely oval, variable, 25-31  $\mu$  broad.

The Carboniferous at Pittsville, Pennsylvania.

2. *C. Clarkei*, Dn.

*Transverse.* Growth rings obscure or entirely wanting. The tracheids about  $41 \times 49 \mu$  broad, their walls  $12.5 \mu$  thick.

*Radial.* Bordered pits numerous throughout the tracheids, in 2-3, more rarely in 4, rows. The elements of the medullary rays of two kinds; the parenchyma cells thin-walled and devoid of pits, about equal to 3 tracheids; the ray tracheids long, interspersed, and bearing on their lateral upper and lower walls numerous crowded, bordered pits.

*Tangential.* Rays very variable, commonly 1-seriate but sometimes 2-seriate in part; the tracheids usually distinguished by their narrow form and pitted walls.

Hamilton Group, Ithaca, New York.

3. *C. Newberryi*, (Dn.) Knowlton

*Transverse.* Tracheids about  $44 \times 55 \mu$ , the walls about  $12.5 \mu$ , thick.

*Radial.* Ray cells resinous and starch bearing, long and narrow, about equal to 3-7 tracheids, the ends conspicuously narrower; the pits on the lateral walls 3-6, chiefly 4, per tracheid, the slitlike orifice nearly the full diameter of the pit. Bordered pits numerous, round, about  $9.3 \mu$  broad, distributed in radially disposed groups of about 6-13; the orifice diagonal, nearly the diameter of the pit.

*Tangential.* Rays of medium height, 1-, 2-, or rarely 3-seriate in part;  $24-55 \mu$  broad, the oval or round cells all thin-walled.

Hamilton Group (Middle Devonian) of Ohio (Newberry); Carboniferous of Ohio (Claypole).

4. *C. recentium*, Dn.

*Transverse.* Tracheids  $47 \times 53 \mu$  broad, the walls much reduced by decay.

*Radial.* Ray cells all of one kind, about equal to 2 tracheids; the lateral walls with round pits about 1 (?) per tracheid; the cells conspicuously narrower at the ends. Bordered pits in a single row, compact, large, compressed, and transversely oval or oblong,  $15.6 \times 22 \mu$ , the orifice very variable from oblong to round, often eccentric, but typically round and central. When distant the pits are round and smaller.

*Tangential.* Rays medium, 1-seriate or 2-seriate, the very broad cells  $41 \mu$ , thin-walled, round, and squarish.

The Permian or Permocarbiniferous of Prince Edward Island.

5. *C. hamiltonense*, Penh.

*Transverse.* Tracheids very variable, growth rings obscure.

*Radial.* Structure of the medullary rays not determinable. Bordered pits hexagonal, in 2 rows throughout.

*Tangential.* Rays numerous and variable,  $31-57 \mu$  broad; the cells very variable in form and size, thin-walled, often broader than high, chiefly 1-seriate, often more or less 2-seriate.

Genesee shales (Hamilton Group) of Ontario County, New York.

6. *C. illinoisense*, Dn.

*Transverse.* Tracheids  $47 \times 47 \mu$  broad, the walls  $9.3 \mu$  thick.

*Radial.* Ray cells straight or abruptly narrowed at the ends, equal to 3-4 tracheids; the lateral walls show no recognizable structure. Bordered pits in 1-3, chiefly 2, rows, hexagonal,  $12.5 \mu$  broad.

*Tangential.* Rays numerous, 1-seriate or 2-seriate in part, the broadly oval, thin-walled cells  $28 \mu$  broad.

Chase Formation (Permian) of Chase County, Kansas; the Coal Measures of Rock Island, Illinois, and Boonsboro, Iowa (?).

7. *C. materioide*, Dn.

*Transverse.* Tracheids about  $56 \times 56 \mu$  broad, the walls  $12.5 \mu$  thick. Scattering tracheids contain resin.

*Radial.* Ray cells straight or somewhat contracted at the ends; the pits on the lateral walls oval, narrowly bordered, 1-8, chiefly 2-3, per tracheid; the lenticular or oblong orifice nearly equal to the diameter of the pit. Bordered pits hexagonal, in 1-3, chiefly 2, rows.

*Tangential.* Rays 1-seriate or sometimes 2-seriate in part, upwards of 35 cells high; the oval or round cells  $25-31 \mu$  broad.

Douglas Mine, Grand Lake, and Mirimichi, New Brunswick; Port Hood and Mabou, Cape Breton; Joggins, Nova Scotia.

8. *C. annulatum*, Dn.

*Transverse.* Structure much altered by decay, extensive areas being completely carbonized and consolidated to coal. The tracheids are about  $34 \times 44 \mu$  broad, the walls much attenuated by decay.

*Radial.* Structure of the rays not determinable. Bordered pits hexagonal,  $9.5 \mu$  broad, in 2-3, chiefly 2, rows.

*Tangential.* The structure is too much altered by decay and pressure to make the details obvious.

Middle Carboniferous, Joggins, Nova Scotia

9. *C. ouangondianum*, Dn.

*Transverse.* Tracheids about  $47 \times 56 \mu$  broad, the walls  $9.3 \mu$  thick. Growth rings none.

*Radial.* Bordered pits numerous throughout the tracheids, in 2-4, chiefly 3, rows, about  $12 \mu$  broad. Ray cells equal to about 3-4 tracheids; the lateral walls with oval pits, 2-4, chiefly 4, per tracheid and disposed in radial series.

*Tangential.* Rays of medium height, 1-seriate or 2-seriate in part, the oval cells chiefly about  $25-37 \mu$  broad.

Middle Devonian of New Brunswick.

10. *C. acadianum*, Dn.

*Transverse.* The large tracheids are about  $62 \times 62 \mu$  broad, the walls  $9.5 \mu$  thick. Scattering tracheids show resinous contents.

*Radial.* Ray cells often somewhat abruptly contracted at the ends, equal to 2-4 tracheids; the lateral walls with numerous round or oval pits, 4-10 per tracheid, chiefly about 6, the border often very narrow, the oblong orifice three fourths the diameter of the pit. Bordered pits numerous, hexagonal,  $12.5-16 \mu$  broad, crowded in 2-5 rows.

*Tangential.* Rays very variable, ranging upwards of 60 cells high, resinous, more or less 2-seriate throughout, the oval or oblong cells  $17-31 \mu$  broad.

Middle Coal Measures, Joggins, Nova Scotia; Port Hood, Mira, and Glace Bay, Cape Breton; Dorchester, New Brunswick; St. George's Bay, Newfoundland.

11. *C. ohioense*, Dn.

*Transverse.* Tracheids  $47 \times 56 \mu$  broad, the walls  $12.5 \mu$  thick.

*Radial.* Ray cells chiefly short, about equal to 2 tracheids, straight, or somewhat abruptly contracted at the ends; the pits on the lateral walls oval, with a prominent border, apparently 2 per tracheid, but not exactly determinable on account of extended decay. Bordered pits in 3-4 rows, sometimes 2 rows throughout the tracheid, hexagonal, about  $12.5 \mu$  broad.

*Tangential.* Rays numerous, upwards of 25 cells high; broad, about  $41 \mu$ , conspicuously squarish, 1- or often 2-seriate or 3-seriate in part.

New Lisbon, Ohio.

12. *C. materiarium*, Dn.

*Transverse.* Tracheids  $45 \times 75 \mu$  broad, the walls  $7.8 \mu$  thick. Scattering tracheids show resinous matter.

*Radial.* Ray cells straight, somewhat narrowed at the ends, equal to about 2-6 tracheids; the pits on the lateral walls large, oval, round, or oblong, narrowly or even obscurely bordered, 1-5, chiefly 1-2, per tracheid. Bordered pits numerous throughout the tracheids, chiefly in 2, sometimes in 3-4, rows, hexagonal, or, when more distant, oval, about  $12.5 \mu$  broad.

*Tangential.* Rays 1-seriate or 2-seriate in part, upwards of 40 cells high, the oval or round cells  $17-35 \mu$  broad.

Holmes County, Ohio (Newberry); Upper Coal Measures of Malagash, Pictou, Joggins, Belen, and Cambon, Nova Scotia; St. George's Bay, Newfoundland; Mirimichi, New Brunswick; Glace Bay, Cape Breton; Marion County, Illinois.

13. *C. Halli*, Dn.

"Wood cells very large, with 5 rows of contiguous, alternate, hexagonal areoles. Medullary rays frequent, and with as many as 30 rows of cells superimposed" (Dawson).

Middle Devonian of Ontario County, New York.

2. \***DAMMARA**,<sup>1</sup> LAMB. PLATES 14 AND 15

*Transverse.* Growth rings more or less clearly defined. Resin-bearing tracheids more or less prominent.

*Radial.* Rays wholly devoid of tracheids. Bordered pits hexagonal in 1-3 rows. Spiral tracheids wanting.

*Tangential.* Medullary rays all of one kind and 1-seriate, usually composed of broad cells.

1. **D. australis**, Steud.

*Kaurie. Cowdie Pine*

*Transverse.* Growth rings very variable and usually poorly defined. Summer wood thin, often obscure, the structure open but the tracheids thick-walled, passing gradually into the spring wood. Spring wood of large, thickish-walled, very variable tracheids with distinctly rounded lumens. Resinous tracheids rather numerous, not very prominent, generally in rows on either side of the medullary rays. Medullary rays prominent, rather resinous, 1 cell wide, not numerous, distant 2-27 rows of tracheids.

*Radial.* Medullary rays devoid of tracheids; the resinous cells strongly contracted at the ends, equal to about 5 spring tracheids; the upper and lower walls thin and not pitted; the terminal walls thin and entire, not locally thickened; the lateral walls with round, bordered pits and a diagonal, lenticular orifice, 2-6 per tracheid. Wood tracheids usually radially thickened opposite the medullary rays, with the development of resinous plates simulating Sanio's bands. Bordered pits hexagonal, chiefly in 2, or more rarely 1-3, rows. Pits on the tangential walls of the summer tracheids very numerous, large, and prominent.

*Tangential.* Fusiform rays wholly wanting. The resinous rays strictly 1-seriate, the cells very broad, unequal, oval or transversely oval, the thin walls often broken out.

3. \***ARAUCARIA**, JUSS. PLATES 16 AND 17

*Transverse.* Growth rings not determinable, or at most poorly defined. Resin passages and specialized resin cells entirely wanting. Resin-bearing tracheids more or less prominent.

*Radial.* Rays wholly devoid of tracheids. Bordered pits usually hexagonal, multiseriate. Spiral tracheids wholly wanting.

*Tangential.* Fusiform rays wholly wanting.

<sup>1</sup> The genus *Protodammara* has been created by Hollick and Jeffrey for the reception of certain cretaceous cones, but at present it does not contain any wood.



## SYNOPSIS OF SPECIES

## I. ARAUCARIA

Existing species confined to the southern hemisphere and unknown in the fossil state.

## A. Growth rings obscure or wanting

Bordered pits in 1-3 rows, hexagonal.

Resin-bearing tracheids (radial) wanting.

## 1. A. Cunninghamii

Resin-bearing tracheids (radial) numerous, the resin in thick plates like Sanio's bands.

## 2. A. excelsa

## B. Growth rings obvious

Bordered pits crowded in 1 row, more or less rounded, not strictly hexagonal.

Rays (radial) locally and strongly resinous, the lateral walls at such points with sieve-plate structure.

## 3. A. Bidwillii

## II. \*\* ARAUCARIOXYLON

Extinct species occurring in Mesozoic and Tertiary strata, the remains being usually silicified or calcified.

## A. Growth rings obscure or wanting

Bordered pits in 1-3 rows.

## 4. \*\* A. Woodworthi.

Bordered pits in 1-2 rows.

## 5. \*\* A. virginianum.

Bordered pits chiefly in 1 row.

Growth rings wholly wanting.

## 6. \*\* A. Prosseri.

Growth rings present but obscure.

## 7. \*\* A. arizonicum.

## B. Growth rings obvious

Bordered pits in 1-2 rows.

## 8. \*\* A. Hoppertonæ.

Bordered pits chiefly in 1 row.

## 9. \*\* A. Edvardianum.

*Araucarioxylon obscurum* of Knowlton (*Mesozoic Floras of the United States*, p. 418) does not belong here at all, but is cited now for future reference.

1. *A. Cunninghamii*, Sweet.

*Moreton Bay Pine. Hoop Pine. Colonial Pine. Coorong. Cumburtu. Cobnam*

*Transverse.* Growth rings not clearly discernible; tracheids very unequal in irregular, radial rows, round-hexagonal, the walls medium; the structure open throughout. Resinous tracheids few, widely scattering. Medullary rays prominent, somewhat resinous, broad, 1 cell wide, distant 2-23 tracheids.

*Radial.* Ray cells conspicuously contracted at the ends, often very unequal, about equal to 10 tracheids; the upper and lower walls thin and not pitted; the terminal walls thin, commonly curved, not pitted or locally thickened; the lateral walls with pits having an obscure border and a slit-like orifice, numerous, 3-8 per tracheid. Bordered pits in 1-2 or 3 rows, compact, compressed, hexagonal. Pits on the tangential walls of the summer tracheids wanting.

*Tangential.* Rays numerous, low to medium, resinous; sometimes 2-seriate in part; the cells very large, unequal, oval or transversely oval, the walls thin.

2. *A. excelsa*, R. Br.

*Norfolk Island Pine*

*Transverse.* Growth rings not determinable; the unequal tracheids in irregular, radial rows, round-hexagonal, the walls medium, the structure open throughout. Resin-bearing tracheids in small, scattered groups, or in rows parallel with the rays on either side. Rays prominent, broad, somewhat resinous, 1 cell wide, distant 2-21 rows of tracheids.

*Radial.* Ray cells conspicuously contracted at the ends, equal to 6-8 tracheids; the upper and lower walls thin, entire; the terminal walls thin, not pitted; the lateral walls with round, bordered pits having a slitlike orifice, about 3-6 per tracheid. Resin-bearing tracheids numerous, the resin in thick plates simulating Sanio's bands in the vicinity of rays. Bordered pits in 1-2 rows, compact, hexagonal.

*Tangential.* Rays medium, numerous, broad; the cells oval or squarish, thin-walled, unequal, the thin walls commonly broken down; 1-seriate.

3. *A. Bidwillii*, Hook.

*Bunya-Bunya*

*Transverse.* Growth rings broad but poorly defined by a slightly more open structure in the early spring wood; the structure rather dense throughout, the unequal tracheids thick-walled, round-hexagonal. Medullary rays not very prominent, locally very resinous, 1 cell wide, distant 4-45 rows of tracheids.

*Radial.* Ray cells rather high and short, equal to upwards of 5 tracheids; distant cells strongly resinous; conspicuously contracted at the ends; the upper and lower walls very thin and entire; the terminal walls thin, entire, commonly curved; the lateral walls with obscurely margined pits; the orifice linear or slitlike, diagonal, 3-7 per tracheid, in the very high, marginal cells forming high, vertical series. Where resin is

deposited the lateral walls of groups of cells bear numerous rounded pits, giving a sieve-plate structure. Bordered pits crowded in 1 row, more or less rounded, not hexagonal, as broad as the narrow tracheids. Pits on the tangential walls of the summer wood wanting.

*Tangential.* Rays low, only a few cells high, numerous, resinous; the cells oval, broad, thin-walled, strictly 1-seriate.

#### 4. \*\* *A. Woodworthi*, Kn.

*"Transverse.* Annual ring very obscure and not visible to the naked eye, but on examination under the microscope it is found to be present and to consist of only 2 or 3 slightly smaller and thicker-walled cells. The wood cells are only moderately thick-walled and are quite uniform in size.

*"Radial.* This section shows to the best advantage the character of the wood. The wood cells are shown to be long, sharp pointed, and to be provided with usually 2 rows of bordered pits, although cells are common on which there is but a single series. Cells on which there are 3 rows of pits are much rarer. When in a single row the pits are contiguous and but slightly modified in shape by pressure. When the pits are in 2 rows they usually occupy the center of the cell and are contiguous and slightly hexagonal; but occasionally the 2 rows may be slightly separated and then may have the characters of the single rows. When there are 3 rows of pits they are close together and markedly hexagonal. The average diameter of the pits is about 0.015 mm., and that of the inner pore about 0.003 or 0.004 mm. The medullary rays, as seen in this section, are short-celled, each cell being about as long as the width of  $2\frac{1}{2}$  wood cells. They are without markings or pits of any kind, so far as can be made out.

*"Tangential.* Owing to pressure in this direction the section is somewhat distorted and does not show clearly the relative abundance of the rays. The number of cells entering into the composition of the rays, however, shows satisfactorily. It is found that they are in a single vertical series of 1-12 cells, the usual number being 3 or 4" (Knowlton).

Material silicified. Specimen from a large, prostrate trunk 20 feet or more in length and over 4 feet in diameter.

Richmond Basin (Trias) south of Mosley Junction, Chesterfield County, Virginia (Knowlton).

#### 5. \*\* *A. virginianum*, Kn.

*"Transverse.* Growth rings not obvious to the naked eye, but apparent microscopically. The line of demarcation consists of only 3 or 4 rows of slightly smaller and thicker-walled cells. [Growth rings obscure, D.P.P.] Tracheids prominent, with thick walls. The individual cells have a diameter of 0.051 mm., the average being about 0.0375 mm. They are arranged in radial rows, which are most pronounced in proximity to the medullary rays.

*"Radial.* The radial walls are the only ones bearing bordered pits. The number of rows varies, even on the same cell, from 1-2. When there is but 1 row they occupy the center of the cell and are in contact. They

are then nearly circular in outline and have a diameter of 0.017–0.02 mm. When there are 2 rows they are in contact and alternate with each other, and have a nearly regular, hexagonal outline. These hexagonal pits have a diameter of 0.016–0.021 mm. The inner pore is very small, being only about .0025–.003 mm. in diameter.

"*Tangential*. The rays are single and range from 1–27 cells in height, the average number being about 10–12" (Knowlton).

Material silicified. Specimen represented by a small fragment.

From the Potomac Formation at Taylorsville, Virginia (Knowlton).

#### 6. \* \* A. Prosseri, Penh.

*Transverse*. Tracheids in regular radial rows, squarish,  $39 \times 42 \mu$  broad; the walls  $6.2 \mu$  thick. Resin cells and special resin passages wholly wanting. No evidence of growth rings in a radial extent of 22 mm.

*Radial*. Ray cells all of one kind, straight or narrower at the ends, equal to 3–9 tracheids; the upper and lower walls thin and devoid of pits; the terminal walls thin, not pitted, curved; the lateral walls show no structure through extreme alteration. Bordered pits not clearly determinable, but probably round and in 1 row.

*Tangential*. Rays numerous, chiefly low; the cells broad, round, about  $31 \mu$  wide.

Material silicified.

The Cheyenne (Comanche Cretaceous) of the bluff west of Sun City, Medicine Lodge River, Baker County, Kansas, 1897 (Prosser).

#### 7. \* \* A. arizonicum, Kn.

"*Transverse*. Annual rings not apparent to the naked eye, but under the microscope observed to be present, the yearly growths being separated by a layer of 2–5 tangentially compressed cells; the tracheids in this section are observed to have moderately thick cell walls, and to be separated by small intercellular spaces. The largest cells observed have a diameter of .055 mm. and the smallest of about .020 mm., the average being about .040 mm.

"*Radial*. As seen in this section the tracheids are observed to be long, and to be provided with numerous pores. These pores or bordered pits are usually arranged in a single series, and number 40–80 or more on each cell. Usually they touch each other slightly, but sometimes they become a trifle compressed by actual contact. When these pores are arranged in 2 series they alternate and are slightly, if at all, angled by mutual pressure. The pores are rather large, the average diameter for the outer circle being about .02 mm., that for the inner .0040 mm. The medullary rays are composed of short, thin-walled cells, which, in some instances, seem to have been provided with small, oval pores. They are difficult of demonstration, and it is possible that the granular contents of the cells may give the appearance of exterior markings.

"*Tangential*. This section demonstrates the presence of pores or bordered pits on the tangential walls, a circumstance of infrequent occurrence

in the genus *Araucarioxylon*. They are much smaller than the pores on the radial walls, and are in a single or rarely in 2 series. The pores are always separated from each other, sometimes widely so. The diameter of the outer circle is about .0075 mm., and that of the inner about .0027 mm. The medullary rays are numerous and range in height from 1-22 cells. It is possible that in some rare cases they may be in 2 series, but this is certainly not commonly the case. No resin ducts have been detected in any of the sections, their absence being a well-known character of the genus" (Knowlton).

Material silicified. Specimens are represented by fragments of trunks upwards of 20 inches in length and 13 inches in diameter.

Triassic or Lower Jurassic near Fort Wingate, New Mexico; *Lithodendron* Creek (Cretaceous?) and Chalcedony Park, Arizona (Knowlton).

#### 8. \* \* A. *Hoppertonæ*, Kn.

"*Transverse*. Annual rings very distinct, of 4-8 rows of very thick-walled fall wood. The spring wood is made up of very large though thick-walled cells, which begin very abruptly at the fall wood. The cells gradually decrease in size until the last 5-8 rows of cells are very thick.

"*Radial*. As the material has been very finely preserved, this section shows remarkably well. The wide cells of the spring wood are provided with usually 2 longitudinal rows of hexagonal pores, which quite cover the walls. Occasionally, in cells of unusual width, the pores, while in 2 series, are only slightly compressed. Usually when but 1 row is present they are hexagonal and occupy the center of the cell. The inner pores in these punctations are relatively small and slightly elongated in a direction at right angles to the cells. The medullary rays as seen in this section are short, covering the width usually of 4 or 5 wood cells, although occasionally longer and covering as many as 8 cells. They are provided with a single row of bordered pores so arranged that 1 comes over each wood cell, or occasionally there may be 2 over a wood cell. The inner pore is minute.

"*Tangential*. The medullary rays as seen in this section are quite numerous, in a single series of from 3 to sometimes as many as 15 superimposed cells. The wood cells as seen in this section do not seem to have been provided with punctations or other markings" (Knowlton).

Material silicified.

Cretaceous formation of the Black Hills, Cycad bed 2 miles southeast of Minnekahta Station, South Dakota (Knowlton).

#### 9. \* \* A. *Edvardianum*, Dn.

"Trunks with distinct rings of growth, and with a central pith not observed to have transverse laminae. Wood cells with 1 or rarely 2 rows of contiguous, hexagonal areolae. Medullary rays simple, infrequent, with 2-10 rows of cells superimposed" (Dawson).

Triassic of Prince Edward Island (Dawson).

## II. GINGKOALES

Wood nonresinous, the tracheids of two kinds, interspersed. Wood parenchyma present and forming idioblasts containing sphere crystals.

## 1. \* GINGKO, KAMPF. PLATES 18 AND 19

*Transverse.* Growth rings broad. The summer wood thin; the structure chiefly open throughout; tracheids chiefly squarish and large, with smaller, thicker-walled tracheids interspersed. Resin passages and resin cells wholly wanting. Crystal-bearing idioblasts rather numerous.

*Radial.* Medullary rays devoid of tracheids. Terminal walls of the ray cells very thin and not pitted. Bordered pits in 1-2 series. Spiral tracheids wholly wanting.

*Tangential.* Fusiform rays wholly wanting. Ray cells rather broad and thin-walled.

1. *G. biloba*, Linn.

*Maidenhair Tree. Salisburia. Gingko. Jap. = Icho*

*Transverse.* Growth rings very broad, the summer wood very narrow and of open structure, passing gradually into the spring wood. Spring wood open, the tracheids large, squarish, very unequal, somewhat thin-walled, with which are interspersed less numerous, much smaller, rounded, and thick-walled tracheids. Idioblasts containing sphere crystals somewhat numerous. Medullary rays prominent, slightly resinous, 1 cell broad, distant 2-10, more rarely 15, rows of tracheids.

*Radial.* Cells of the medullary rays conspicuously contracted at the ends, locally somewhat resinous, equal to about 5-7 spring tracheids; the upper and lower walls very thin and not pitted; the terminal walls very thin, not pitted or locally thickened, chiefly straight; the lateral walls with oval, bordered pits having a narrowly oval or oblong orifice, about 1-4, or, in the marginal cells, 7, per tracheid. Bordered pits very numerous in the broader tracheids, where they are compressed vertically and crowded in 1 row, or more generally in pairs, forming 2 compact series; in the narrower tracheids few, round, distant, and often wanting. Pits on the tangential walls of the summer tracheids numerous, large, and open. Idioblasts round or oblong, 1 sphere crystal to each; scattering or often in vertical series.

*Tangential.* Fusiform rays wholly wanting. Rays strictly 1-seriate, low to medium; the cells rather broad, oval, thin-walled, somewhat variable. Idioblasts oblong, in vertical series.

Native of Japan, now widely distributed through cultivation in similar climates.

2. \*\* *G. pusilla*, Dn.

*Transverse.* Growth rings obvious, the spring wood passing gradually into the not strongly defined summer wood; tracheids in regular radial rows, very uniform, those of the spring wood about  $22 \times 21 \mu$ , the walls  $5.3 \mu$  thick. Medullary rays very narrow.

*Radial.* Medullary rays very low, the cells straight, about  $17\ \mu$  high, equal to about 5 tracheids; the upper and lower walls thin and not pitted; the terminal walls thin, straight, and devoid of pits; the lateral walls with large (?) pits, 1 per tracheid. Bordered pits on the radial walls of the tracheids not recognizable.

*Tangential.* Medullary rays 1-3, more rarely 4, cells high, about  $8.7\ \mu$  broad.

Material calcified.

Upper Cretaceous of Port McNeil, Vancouver Island, and Upper Cretaceous of Cumshava Inlet, Queen Charlotte Islands.

### III. CONIFERALES

Wood more or less resinous, often characterized by the presence of specialized resin cells, cysts, or passages. Tracheids (transverse) in radial rows, bearing on their radial walls, as also on the tangential walls of the summer tracheids, round or elliptical, often distant, bordered pits in 1-3 series.

#### 1. *TORREYA*, ARNOTT. PLATES 20 AND 21

*Transverse.* Growth rings rather thin, often variable; tracheids rather large, chiefly squarish, the structure generally open throughout. Summer wood usually very thin. Resin cells and resin passages wholly wanting.

*Radial.* Ray cells very long, the tracheids of the wood with rather open spirals in 2-4 series.

*Tangential.* Ray cells large, broadly oval or oblong. Fusiform rays wholly wanting.

#### SYNOPSIS OF SPECIES

*A.* Summer wood thin, of 2-4 tracheids or more, often double; the structure of the growth ring very open throughout

Tracheids large, distinctly squarish.

Spirals in 2 series.

1. *T. taxifolia*.

*B.* Summer wood thin but sometimes equal to the spring wood

Tracheids very unequal, not conspicuously squarish, chiefly hexagonal, often in very irregular rows.

Spirals imperfectly 2-4 seriate, often very incomplete.

2. *T. californica*.

Spirals in double, triple, or quadruple series.

3. *T. nucifera*.

1. *T. taxifolia*, Arnott*Stinking Cedar. Savin*

*Transverse.* Growth rings variable, 1.5–3 mm. thick. Summer wood of 2–4 or more tracheids, usually very thin, often double and passing gradually into the spring wood; spring tracheids squarish and in regular rows, rather uniform. Structure of the growth ring open throughout. Medullary rays somewhat prominent, 1 cell wide, distant 2–9, rarely 16, rows of tracheids.

*Radial.* Ray cells straight; the upper and lower walls thick, conspicuously pitted, uniform; the terminal walls thin and entire, sometimes curved; the lateral walls with small, round, but variable pits with a distinct border, the orifice very narrow, 2–5 per tracheid. Bordered pits in 1 or 2 rows. Pits on the tangential walls of the summer tracheids obscure. Spirals of the tracheids in 2 series, distant 5–30  $\mu$ , very flat, the angle 70.4°, compact and finally vestigial in the summer wood.

*Tangential.* Rays medium, the cells rather small, oval, or oblong, thick-walled.

Very durable in the soil.

Relative specific gravity . . . . .	0.5145
Approximate fuel value . . . . .	51.08
Coefficient of elasticity in kilograms on millimeters. . . . .	821.
Ultimate transverse strength in kilograms . . . . .	378.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7364.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2523.
(Sargent)	

Western Florida.

2. *T. californica*, Torr.*Stinking Cedar. California Nutmeg*

*Transverse.* Growth rings 1.5–2.5 mm. broad. Summer wood thin, sometimes one fourth to one half the spring wood into which it passes gradually. Structure of the growth rings rather open throughout, the tracheids somewhat rounded and in more or less irregular rows. Medullary rays rather prominent, 1 cell wide, distant 2–14 rows of tracheids.

*Radial.* Ray cells straight; the upper and lower walls rather thin, conspicuously double and frequently pitted; the terminal walls very thin and entire; the lateral walls with rather variable, round, bordered pits, 1–6 per tracheid, the orifice very narrow. Bordered pits usually somewhat distant, elliptical, in 1 row, sometimes in pairs. Pits on the tangential walls of the summer tracheids small and obscure. Spirals of the tracheids high, often very incompletely developed, imperfectly 2–4 seriate, distant 5–125  $\mu$  or more, the angle 46.2°, in the summer wood obscure and finally obsolete.

*Tangential.* Rays medium to low, the cells large, rather thin-walled.



Very durable in the soil.

Relative specific gravity . . . . .	0.4760
Approximate fuel value . . . . .	46.96
Coefficient of elasticity in kilograms on millimeters . . . . .	401.
Ultimate transverse strength in kilograms . . . . .	249.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5625.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1962.
(Sargent)	

Mendocino County, California, and along the western slope of the Sierra Nevadas to Tulare County, at elevations of 3000–5000 feet (Sargent).

### 3. *T. nucifera*, Sieb. et Zucc.

*Jap.* = *Kaya*

*Transverse.* Growth rings rather narrow; the tracheids of the spring wood large, often distinctly squarish, passing gradually into the conspicuous but narrow summer wood of about 10 tracheids, which again becomes equal to the spring wood. Medullary rays prominent, 1 cell wide, distant 2–10 rows of tracheids.

*Radial.* Cells of the medullary rays not contracted at the ends, equal to about 6 tracheids; the upper and lower walls medium, remotely and obscurely pitted; the terminal walls thin, not pitted or locally thickened, diagonal or straight, rarely curved; the lateral walls with small, conspicuously bordered, oval pits with a diagonal, linear-oblong orifice, about 2–6, or, in the summer wood, 1 per tracheid. Bordered pits in 1 series, or in pairs, forming 2 imperfect series, distant, the outer margin rather obscure, the orifice lenticular and diagonal throughout. Pits on the tangential walls of the summer wood wholly wanting. Spirals of the tracheids prominent, distant 5–25  $\mu$ , in double, triple, or quadruple series, the angle 70.5°, in the summer wood becoming vestigial in the outer tracheids.

*Tangential.* Rays numerous, low to medium, the walls of the cells rather thick. Pits on the tangential walls of the summer wood wanting.

Japan.

### 2. \* *TAXUS*, TOURN. PLATES 22 AND 23

*Transverse.* Growth rings variable, often unconformable. The summer wood dense and conspicuous, though often very thin; the tracheids small throughout and more or less rounded, the structure somewhat dense or more rarely open (*T. floridana*), with large and squarish tracheids. Resin passages and resin cells wholly wanting.

*Radial.* Spirals of the tracheids rather close, 2-, rarely 3-seriate.

*Tangential.* Ray cells narrowly oblong. Fusiform rays wholly wanting.

## SYNOPSIS OF SPECIES

### A. Tracheids small, rounded, thick-walled

Rays low, 1-seriate.

Growth rings variable, sometimes double.

#### 2. \* *T. canadensis*, Willd.

Rays chiefly high, 1-2 seriate.

Growth rings usually broad.

3. *T. brevifolia*, Nutt.

*B.* Tracheids medium, rather thick-walled

Rays medium.

Growth rings usually rather broad.

4. *T. cuspidata*, Sieb. et Zucc.

*C.* Tracheids large, the structure open

Rays chiefly high.

1. *T. floridana*, Nutt.

1. *T. floridana*, Nutt.

*Yew*

*Transverse.* Growth rings medium, irregularly eccentric. Summer wood very thin, upwards of 10 tracheids thick, rarely double, open; the tracheids unequal in irregular rows with more or less conspicuous intercellular spaces; transition to the spring wood gradual. Medullary rays prominent, 1 cell wide, distant 1-10 rows of tracheids.

*Radial.* Ray cells straight, rather narrow; the upper and lower walls entire, more or less sinuately unequal; the terminal walls thin and not pitted; the lateral walls with somewhat conspicuously bordered oval or rounded pits, the orifice lenticular, diagonal, chiefly 1-2, more rarely 3, or, in the marginal cells, 4 per tracheid. Bordered pits very scattering except at the ends of tracheids, where they become more or less 2-rowed. Pits on the tangential walls of the summer wood small, often very distant, the orifice bell-shaped. Spirals of the tracheids prominent, rather flat, 2-seriate, distant 7.5-20  $\mu$ , rarely more, the angle 78.4°, wanting in the outer summer wood.

*Tangential.* Rays medium to high, the cells very narrowly oval to oblong. Western Florida.

2. \* *T. canadensis*, Willd.

*American Yew. Ground Hemlock*

*Transverse.* Growth rings narrow and variable, often unconformable. Summer wood variable, now thin and abruptly passing into the spring wood, or thickish and finally equal to the spring wood into which it gradually passes; rather dense. Spring wood more open, the tracheids small throughout and thick-walled but distinctly rounded and variable. Medullary rays 1 cell wide, not very prominent, distant 2-15 tracheids.

*Radial.* Ray cells equal to about 5 spring tracheids; the upper and lower walls rather thin, uniform, entire, or remotely pitted; the terminal walls thin and entire, often curved; the lateral walls with round, bordered pits, 1-2 per tracheid. Bordered pits small, round. Pits on the tangential walls of the summer wood very numerous but small and obscure. Spirals of the tracheids very prominent, 2-3 seriate, distant 7.5-15  $\mu$ , the angle 72.4°, conspicuous throughout the summer wood.

*Tangential.* Rays very low, the cells rather thick-walled.

Damp woodlands from Newfoundland westward to Lake Winnipeg and Minnesota, northward to York Factory, and southward to New Jersey or along the Alleghenies to Virginia.

The Pleistocene of the Don River, Toronto; Solsgirth and Heart Hill, Rolling River, Manitoba, and Fort Madison, Iowa; Cape Breton and Bloomington, Illinois. An abundantly represented and widely distributed species in the northern United States and southern Canada.

### 3. *T. brevifolia*, Nutt.

*Yew. Western Yew*

*Transverse.* Growth rings thick, upwards of 2–3 mm. Summer wood dense, about equal to the spring wood into which it passes very gradually. Spring wood open, the tracheids in regular rows, rather uniform, not much rounded. Medullary rays 1 cell wide, distant about 1–17 rows of tracheids.

*Radial.* Ray cells very long; the upper and lower walls thickish, unequal, conspicuously double, entire or distantly pitted; the terminal walls thin and entire; the lateral walls with round, conspicuously bordered pits, chiefly 2, more rarely 4, per tracheid, the narrow diagonal orifice equal to the outer ring. Bordered pits round or elliptical. Pits on the tangential walls of the summer tracheids numerous but very small and obscure. Spirals of the tracheids prominent, 2-seriate, distant 7.5–20  $\mu$ , rarely more, the angle 63.0°, vestigial in the summer wood.

*Tangential.* Rays commonly high, the cells thick-walled.

Very durable in the soil.

Relative specific gravity . . . . .	0.6391
Approximate fuel value . . . . .	63.78
Coefficient of elasticity in kilograms on millimeters . . . . .	761.
Ultimate transverse strength in kilograms . . . . .	460.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7734.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	4223.
(Sargent)	

Vancouver Island and adjacent mainland and on the lower Skeena (Macoun); sparingly in the Queen Charlotte Islands (Dawson); southward through the coast ranges of British Columbia, Washington, and Oregon, the western slopes of the Rocky Mountains in Montana, and through the California coast ranges to Monterey and the southern slopes of the Sierra Nevadas to latitude 37° N. (Sargent).

### 4. *T. cuspidata*, Sieb. et Zucc.

*Yew. Jap. = Araragi*

*Transverse.* Growth rings rather broad. Summer wood prominent, about one fourth the spring wood into which it passes gradually. Spring wood somewhat open, the tracheids distinctly hexagonal, rather

uniform and thin-walled. Bordered pits on the tangential walls of the summer tracheids few and obscure. Medullary rays prominent, 1 cell wide, distant about 2–10 tracheids.

*Radial.* Cells of the medullary rays not much contracted at the ends; the upper and lower walls rather thin, but very unequal and obscurely pitted; the terminal walls thin, often obscure, not pitted or locally thickened, diagonal and chiefly straight; the lateral walls with conspicuously bordered pits, oval, with a diagonal, lenticular-oblong orifice, chiefly 2 per tracheid in radial series, equal to about 4–9 tracheids. Bordered pits round, about two thirds the width of the tracheid, in open rows, the orifice round, concentric, in the summer wood becoming lenticular, diagonal. Pits on the tangential walls of the summer tracheids distant, rather obscure. Spirals of the tracheids 2-seriate, distant 12.5–25  $\mu$ , the angle 66.1°, vestigial in the summer wood.

*Tangential.* Bordered pits on the tangential walls of the summer tracheids not very numerous, in distant groups. Rays low to high, numerous.

### 3. THUJOPSIS, SIEB. ET ZUCC. PLATES 24 AND 25

*Transverse.* Growth rings usually very narrow. Resin passages wholly wanting. Resin cells not numerous but prominent, rarely zonate.

*Radial.* Ray tracheids wholly wanting. Bordered pits generally rather numerous, in 1 row. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting, the 1-seriate rays low, resinous.

#### 1. *T. dolabrata*, Sieb. et Zucc.

*Jap.* = *Hiba*

*Transverse.* Growth rings very narrow and variable. Summer wood rather open, sometimes dense, thin, of 2–10 tracheids, the transition to the spring wood rather gradual. Spring wood very open, the tracheids large, squarish-hexagonal, in very regular rows, uniform, very thin-walled. Resin cells very prominent, not numerous, scattering throughout the growth ring, not obviously zonate. Medullary rays prominent and resinous, not numerous, 1 cell wide, distant 2–12 or sometimes 16 rows of tracheids.

*Radial.* Rays somewhat resinous. The cells conspicuously contracted at the ends, equal to 5–6 spring tracheids; the upper and lower walls thick, sparingly pitted; the terminal walls thin, often curved, not pitted or locally thickened; the lateral walls with small, obscurely bordered pits, the large orifice broadly lenticular or oval, about 1–2 per tracheid. Bordered pits round or elliptical, nearly as broad as the tracheid, rather numerous, in 1 row. Pits on the tangential walls of the summer tracheids few, very flat, and rather obscure. Resin cells 15–25  $\mu$  wide, chiefly 225  $\mu$  long.

*Tangential.* Rays low, not very broad, resinous; the cells oval or oblong, rarely round, rather thick-walled, 1-seriate.

4. **CRYPTOMERIA**, DON. PLATES 26 AND 27

*Transverse.* Growth rings medium, with a dense summer wood and open spring wood. Resin passages wholly wanting. Resin cells prominent and scattering.

*Radial.* Rays wholly devoid of tracheids; the cells sparingly, if at all, resinous; the terminal walls thin and not pitted or locally thickened. Bordered pits in 1 row, much less than the diameter of the tracheid.

*Tangential.* Fusiform rays wholly wanting. Cells of the 1-seriate rays rather broad, round.

1. **C. japonica**, Don.

*Cryptomeria. Jap. = Sugi*

*Transverse.* Growth rings medium, rather uniform. The summer wood prominent, about one fourth the spring wood into which it passes rather abruptly, the structure dense. Spring wood very open, the large tracheids hexagonal, uniformly thin-walled. Resin cells prominent and scattering, chiefly confined to the summer wood and the late spring wood, the resin filling the cells. Medullary rays somewhat prominent, distant 2-14, more rarely 20, rows of tracheids.

*Radial.* Ray cells more or less contracted at the ends, equal to 5-9 spring tracheids; the upper and lower walls rather thick, uniform, distantly pitted; the terminal walls thin, not pitted or locally thickened, straight or curved; the lateral walls with round, obscurely bordered pits, 1-2 in radial series or in the marginal cells 3-5 per tracheid. Bordered pits one half the diameter of the tracheid, in 1 row, round, the orifice round; in the summer wood small, becoming obscure or entirely wanting, the orifice a slit. Pits on the tangential walls of the summer tracheids small but numerous. Resin cells upwards of 20  $\mu$  wide and upwards of 400  $\mu$  long.

*Tangential.* Rays all 1-seriate, rarely 2-seriate in part; low, the cells round, rather thick-walled, uniform.

5. **PODOCARPUS**, L'HER. PLATES 28 AND 29

*Transverse.* Growth rings very variable, either very narrow or very broad. Summer wood very thin and not clearly distinguishable from the spring wood. Structure open, tracheids of the spring wood large, squarish. Resin passages wholly wanting. Resin cells numerous, scattering, rarely zonate.

*Radial.* Ray tracheids wholly wanting. Bordered pits small, distant in 1 row. Spiral tracheids wholly wanting.

*Tangential.* Fusiform rays wholly wanting. Ray cells oval or round, thick-walled.

1. **P. macrophylla**, Don.

*Jap. = Maki*

*Transverse.* Growth rings very variable and narrow, or again broad. The summer wood very thin and not very different, of 2-4 tracheids and passing imperceptibly into the spring wood. Tracheids of the spring

wood chiefly rectangular, rather uniform, and somewhat thick-walled. Resin cells very numerous, the resin chiefly in a peripheral layer; scattering throughout the growth ring or occasionally becoming more or less zonate. Medullary rays prominent, numerous, and 1 cell wide, distant 2-9 rows of tracheids.

*Radial.* Medullary rays conspicuously resinous, numerous; the cells not much contracted at the ends, equal to about 6 tracheids. The upper and lower walls thickish, unequal, irregularly and often distantly pitted, the pits rather broad; the terminal walls thin, not pitted or locally thickened, chiefly strongly curved; the lateral walls with small, rather obscure, oval pits, 1-2 per tracheid, the orifice narrowly lenticular, often slitlike. Resin cells very numerous, upwards of 20  $\mu$  wide and 200  $\mu$  long. Bordered pits small, round, distant in 1 row. Pits on the tangential walls of the summer wood numerous, conspicuous, open.

*Tangential.* The 1-seriate rays very numerous, medium; the oval or round cells somewhat thick-walled, rarely in pairs.

#### 6. \* TAXODIUM, RICH. PLATES 30 AND 31

*Transverse.* The summer wood of the usually broad growth rings much less than the spring wood. Resin passages wholly wanting. Resin cells numerous and prominent, either scattering or zonate.

*Radial.* Rays wholly without tracheids, the cells commonly contracted at the ends. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting, the cells of the 1-seriate rays broadly oval.

#### SYNOPSIS OF SPECIES

Resin cells large, numerous, more or less distinctly zonate.

Pits on the lateral walls of the rays cells 1-4, more rarely 7, per tracheid, the lenticular orifice narrow.

Bordered pits numerous, often paired, or in the earlier spring wood imperfectly 2-rowed.

##### 1. \* T. distichum.

Resin cells obscure and forming an open zone on the inner face of the summer wood.

Pits on the lateral walls of the ray cells about 2-3 per tracheid in radial series.

Bordered pits numerous, in the earlier spring wood crowded into 2-3 compact rows, but becoming 2-rowed toward the summer wood.

##### 2. \* \* T. laramianum.

##### 1. \* T. distichum, Rich.

*Bald Cypress. Deciduous Cypress*

*Transverse.* Growth rings usually very broad. The dense and conspicuous summer wood often double or treble; transition to the spring

wood somewhat gradual. Spring wood very open; the tracheids very large, thin-walled, hexagonal, rather uniform. Resin cells numerous, large, not strongly resinous, distinctly zonate or sometimes scattering throughout the growth ring. Medullary rays prominent but sparingly resinous, distant 2-8 or more rarely 13 rows of tracheids, 1 cell wide.

*Radial.* Ray cells sparingly resinous, usually more or less contracted at the ends, equal to 3-5 spring tracheids; the upper and lower walls thickish, rather unequal and entire or distantly and often imperfectly pitted; the terminal walls thin, sometimes obscure, often curved, not pitted or locally thickened; the lateral walls with prominent and conspicuously bordered pits, round, 1-4, or more rarely 7, per tracheid, the very narrow, lenticular orifice often as long as the outer limits of the pit. Bordered pits chiefly elliptical, numerous, variable, often paired and in the earlier spring wood becoming imperfectly 2-seriate. Pits on the tangential walls of the summer tracheids very numerous, not very large. Resin cells sparingly resinous, 25  $\mu$  wide, chiefly 140  $\mu$  long, but ranging upwards of 310  $\mu$ .

*Tangential.* Rays numerous, medium to high, very sparingly resinous; the round or oval cells rather broad and thick-walled, rarely in pairs.

Wood very durable in the soil and of great economic value.

Relative specific gravity . . . . .	0.4543
Approximate fuel value . . . . .	45.24
Coefficient of elasticity in kilograms on millimeters . . .	1032.
Ultimate transverse strength in kilograms . . . . .	291.
Ultimate resistance to longitudinal crushing in kilograms .	6771.
Resistance to indentation to 1.27 mm. in kilograms . . .	1166.
(Sargent)	

Material silicified.

Delaware to Florida and westward through the Gulf States to Texas; northward through Tennessee, Kentucky, and southern Missouri to southern Illinois and Indiana (Sargent).

This well-known Tertiary plant, chiefly represented by its foliage and fruit, is known through its woody structure in only one instance, occurring in the Eocene of the Porcupine Creek and Great Valley groups.

## 2. \* \* *T. laramianum*, Penh.

*Transverse.* Growth rings prominent, rather broad. Summer wood prominent, upwards of 17 tracheids thick and passing somewhat gradually into the broad spring wood. Spring tracheids large, squarish-hexagonal, thin-walled, uniform in regular rows. Resin cells obscure and forming an open zone on the inner face of the summer wood. Resin passages wholly wanting. Medullary rays numerous, narrow, distant about 2-8 rows of tracheids.

*Radial.* Medullary rays wholly devoid of tracheids. Ray cells straight, equal to about 3 tracheids; the upper and lower walls rather thick

and sparingly pitted; the terminal walls straight or diagonal, sometimes curved, entire; the lateral walls with oval or rounded pits, about 2-3 per tracheid in radial series. Bordered pits numerous, but becoming 2-rowed toward the summer wood, though distinctly crowded into 2-3 compact rows in the earlier spring tracheids. Resin cells not conspicuous.

*Tangential.* Resin cells conspicuous but not numerous, about 3 times longer than broad. Medullary rays rather numerous and narrow, often very high, strictly 1-seriate; the cells oval, more rarely round in the low rays.

Material silicified.

A distinctive species occurring in the Laramie (Eocene) at Cochrane, Alberta.

## 7. LIBOCEDRUS, ENDL. PLATES 32 AND 33

*Transverse.* The thin and rather dense summer wood usually showing a more dense median layer. Resin passages wholly wanting. Resin cells numerous and conspicuously zonate.

*Radial.* Rays wholly without tracheids. The terminal walls of the ray cells straight or curved, entire, locally thickened or even coarsely pitted. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting, the rays strictly of one kind.

### 1. *L. decurrens*, Torr.

*White Cedar. Bastard Cedar. Post Cedar. Incense Cedar*

*Transverse.* Growth rings broad. The dense summer wood rather thin and composed of 8-14 tracheids, often more or less double; the transition from the spring wood gradual. Spring tracheids in regular rows, uniform, squarish, large and thin-walled, the structure open. Resin cells numerous, prominent, large, in a very broad band or scattering through the late spring wood. Medullary rays prominent, numerous, resinous, 1 cell wide; distant 2-8, rarely 15, rows of tracheids.

*Radial.* Ray cells sparingly resinous, more or less contracted at the ends, equal to about 4-8 spring tracheids; the upper and lower walls medium and entire, or again distantly and often imperfectly pitted; the terminal walls thin, straight, or curved and locally thickened or even coarsely pitted; the lateral walls with small, narrowly bordered, oval pits with a lenticular, diagonal orifice, 1-4 per tracheid. Bordered pits in 1 row, sometimes in pairs, numerous. Pits on the tangential walls of the summer tracheids numerous and large, extending almost through the entire zone. Resin cells 20-30  $\mu$  wide, chiefly 175-225  $\mu$  long, less commonly upwards of 475  $\mu$ .

*Tangential.* Rays very variable, often 2-3 seriate at the center or near one end, sparingly resinous, rather broad; the cells round or oval, uniform, the walls medium.



A large tree 30-40 m. in height, with a trunk 1.20-2.10 m. in diameter. The light, soft wood is very durable in contact with the soil.

Relative specific gravity . . . . .	0.4017
Approximate relative fuel value . . . . .	40.14
Coefficient of elasticity, in kilograms on millimeters . . . . .	847.
Ultimate transverse strength in kilograms . . . . .	291.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7446.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1561.
(Sargent)	

Santian river, Oregon; southward along the western slopes of the Cascade and Sierra Nevada mountains at elevations of 3000-8500 feet, thence through California Coast Range to the San Bernardino and Cayumaca mountains (Sargent).

### 8. \* *THUYA*, TOURN. PLATES 34 AND 35

*Transverse.* Summer wood thin and dense. Resin passages wholly wanting. Resin cells more or less prominent, but often widely scattering. Tracheids chiefly large and thin-walled, squarish.

*Radial.* Ray tracheids wholly wanting except in *T. japonica*. Ray cells usually conspicuously contracted at the ends; the terminal walls thin and not pitted or locally thickened, usually much curved. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting. Ordinary rays narrow, medium to low, strictly 1-seriate, the cells chiefly narrowly oval to oblong.

### SYNOPSIS OF SPECIES

Pits on the lateral walls of the ray cells 1-2, or in the marginal cells and low rays upwards of 8 per tracheid.

Pits on the tangential walls of the summer wood confined to the outermost wall.

#### 3. *T. japonica*, Max.

Pits on the lateral walls of the ray cells 1-4, or in the marginal cells and low rays 6 per tracheid.

Pits on the tangential walls of the summer wood not confined to the outermost tracheid wall.

#### 1. *T. gigantea*, Nutt.

Pits on the lateral walls of the ray cells 1-4, or in the marginal cells and low rays 7 per tracheid.

Pits on the tangential walls of the summer wood confined to the outermost tracheid wall.

#### 2. \* *T. occidentalis*, Linn.

1. *T. gigantea*, Nutt.*Red Cedar. Canoe Cedar. Western White Cedar*

*Transverse.* Growth rings usually broad. Summer wood prominent and upwards of 14 tracheids thick, the transition to the spring wood gradual. Spring wood open, the thin-walled tracheids squarish-hexagonal, rather uniform, in regular rows. Resin cells usually in a single narrow band in the summer wood of distant growth rings, thus often apparently wanting. Medullary rays somewhat resinous, 1 cell wide, distant 2-20 tracheids.

*Radial.* Rays devoid of tracheids, somewhat resinous. Ray cells conspicuously contracted at the ends; the upper and lower walls thickish and entire or remotely pitted; the terminal walls thin, generally curved, not pitted or locally thickened; the lateral walls with small, oval pits with a lenticular or oval orifice, 1-4, or in the marginal cells and low rays 6 per tracheid. Bordered pits round, in one row, sometimes in pairs. Pits on the tangential walls of the summer wood small, conspicuous, often remote, not confined to the outermost wall.

Resin cells about 15  $\mu$  wide, 60-255  $\mu$  long, very variable, thin-walled.

*Tangential.* Rays medium, narrow, the cells oblong.

A light, soft, and rather brittle wood which is very durable in the soil.

Relative specific gravity . . . . .	0.3796
Approximate relative fuel value . . . . .	37.90
Coefficient of elasticity in kilograms on millimeters . . . . .	1034.
Ultimate transverse strength in kilograms . . . . .	319.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7197.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1114.
(Sargent)	

Alaska, southward through the coast ranges of British Columbia, where it attains to an altitude upwards of 6000 feet, often attaining a height of 150 feet and a diameter of more than 10 feet (Macoun); thence through Washington, Oregon, and California, as far as Mendocino County, and eastward through Washington and Idaho to northern Montana (Sargent).

2. \* *T. occidentalis*, Linn.*White Cedar. Arbor Vite*

*Transverse.* Growth rings chiefly broad but variable. Summer wood very thin, of 2-6 or upwards of 14 tracheids, the structure very open, the tracheids large and squarish-hexagonal, in regular rows, rather uniform, thin-walled. Resin cells few and widely scattering, often apparently wanting, or sometimes distantly zonate in the spring wood. Medullary rays not prominent, 1 cell wide, distant 2-15 tracheids.

*Radial.* Rays devoid of tracheids, sparingly, if at all, resinous. Ray cells more or less contracted at the ends; the upper and lower walls medium, with conspicuous though often distant pits; the terminal walls thin, often strongly curved, not pitted or locally thickened;

the upper and lower walls medium, with conspicuous, though often distant, simple pits; the lateral walls with small, oval pits with an oval or lenticular, rather large, orifice, 1-4, or in the marginal cells and low rays 7 per tracheid. Bordered pits elliptical in one row, sometimes in pairs, those of the summer wood finally obscure and wanting. Pits on the tangential walls of the summer wood small, often obscure, frequently very distant and confined to the outermost tracheid wall. Resin cells 15-40  $\mu$  wide.

*Tangential.* Rays low and narrow, the cells uniformly narrow, oblong.

A tree 12-18 m. in height and 1.20-1.50 m. in diameter, producing a light, soft, and very durable wood.

Relative specific gravity . . . . .	0.3164
Approximate relative fuel value . . . . .	31.53
Coefficient of elasticity in kilograms on millimeters . . . . .	533.
Ultimate transverse strength in kilograms . . . . .	219.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4903.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	957.

(Sargent)

Rare in Nova Scotia; abundant in New Brunswick, Quebec, and Ontario, and northward to Hudson's Bay; westward to Lake Winnipeg and the mouth of the Saskatchewan in latitude 53° 30' N. (Macoun); southward to New Jersey and through the Alleghenies to North Carolina (Britton); thence westward through New York and Pennsylvania to central Michigan, northern Illinois, and central Minnesota (Sargent).

This species is a well-defined and somewhat abundant constituent of the Pleistocene flora in the Don Valley at Toronto, and the Leda clays of Montreal; Leda River, Manitoba, and Marietta, Ohio. An undescribed species of *Thuja* also occurs in the Lignite Tertiary, Saskatchewan, probably of the Porcupine Creek and Great Valley groups.

### 3. *T. japonica*, Max.

*Jap.* = *Nedsuko*

*Transverse.* Growth rings rather narrow, variable; the prominent summer wood very narrow, of about 6 tracheids, or again upwards of 16 tracheids, rather dense, the transition to the spring wood gradual. The broad spring wood open; the tracheids rather large, conspicuously hexagonal, very thin-walled, in regular rows, uniform. Resin cells prominent and dark, few and widely scattering, chiefly in the summer wood. Medullary rays not prominent, sparingly resinous, 1 cell wide, narrow, distant 2-18 tracheids.

*Radial.* Rays very sparingly resinous, rarely with tracheids. Cells chiefly straight, the upper and lower walls rather thin, uniform, and frequently pitted; the terminal walls thin, very commonly curved, not

pitted or locally thickened; the lateral walls with small, oval pits, the orifice broadly lenticular, 1-2 or in the marginal cells and low rays upwards of 8 per tracheid. Bordered pits elliptical in one row, sometimes in pairs, numerous, about one half the diameter of the tracheid. Pits on the tangential walls of the summer wood confined to the outermost wall, not large, flat, rather numerous, often obscure. Resin cells few,  $12.5\ \mu$  wide, about  $135\ \mu$  long.

*Tangential.* Rays low to medium, very narrow, strictly 1-seriate; the cells uniform, thin-walled, oblong.

#### 9. \* SEQUOIA, ENDL. PLATES 36 AND 37

*Transverse.* Growth rings chiefly narrow, the usually thin summer wood distinct. Resin cysts when present forming a continuous row on the outer face of distant growth rings. Tracheids large, thin-walled, square. Resin cells scattering, chiefly in the spring wood, or more rarely wholly in the summer wood (*S. Penhallowii*).

*Radial.* Rays without tracheids, but the marginal cells sometimes crystallogenous (*S. Penhallowii*). Pits of the ray cells with a narrow border, the orifice commonly parallel with the cell axis. Pits often occur on the tangential walls of both spring and summer tracheids. Terminal walls of the ray cells rarely, if at all, pitted, except in *S. Penhallowii*. Tracheids wholly without spirals. Radial resin passages wanting except in *S. Burgessii* and *S. Penhallowii*, when they contain prominent thyloses.

*Tangential.* Fusiform rays usually wanting, or present in *S. Burgessii* and *S. Penhallowii*.

#### SYNOPSIS OF SPECIES

Resin passages wholly wanting.

Resin cells more or less numerous and scattering throughout the growth ring.

Bordered pits large, oval, conspicuously in 1-2 rows.

Ray cells (tangential) of the spring wood very large and broad, squarish.

Pits on the lateral walls of the rays cells 2-6 per tracheid.

1. *S. sempervirens*.

Bordered pits in 1 or sometimes 2 rows.

Ray cells (tangential) large, broad, squarish, or as often transversely oblong.

5. \* \* *S. magnifica*.

Ray cells (tangential) broadly oval or round.

Pits on the lateral walls of the ray cells 1-2, or rarely 3-4, per tracheid.

2. *S. gigantea*.

Resin cells on the outer face of the summer wood only.

Bordered pits not definitely seriate.

Pits on the lateral walls of the ray cells 1-seriate in the central, 2-3 seriate in the marginal cells which are crystallogenous.

6. \* \* S. Penhallowii.

Resin passages present on the outer face of the summer wood.

Resin cells more or less numerous and scattering throughout the growth ring.

Bordered pits in 1-2 rows.

Ray cells (tangential) very large and *broad, squarish*.

Pits on the lateral walls of the ray cells 2-6 per tracheid.

1. S. sempervirens.

Ray cells (tangential) oval or round.

Pits on the lateral walls of the ray cells obliterated.

3. \* \* S. Langsdorfii.

Resin passages (radial only) with thyloses.

Resin cells somewhat numerous, scattering throughout the growth ring but most abundant on the outer face of the summer wood.

Bordered pits in 1-2 rows.

Marginal ray cells not crystallogenous.

4. \* \* S. Burgessii.

Resin passages (traumatic) present, both vertically and radially.

Resin cells on the outer face of the summer wood only.

Bordered pits not definitely seriate.

Pits on the lateral walls of the ray cells 1-seriate in the central, 2-3 seriate in the marginal cells which are crystallogenous.

6. \* \* S. Penhallowii.

### 1. S. sempervirens, Endl.

#### *Redwood*

*Transverse.* Summer wood very prominent, of 3-11 tracheids, or upwards of one third the spring wood; the structure often very open, or when dense sometimes double. Spring wood very open, the large, squarish, or hexagonal tracheids often radially elongated, the walls thin; transition to the summer wood rather abrupt. Resin cysts contiguous and coalescent and forming an extended tangential series in the initial growth of the spring wood, of distant growth rings. Resin cells rather abundant, very prominent and dark, rather large, scattering through the spring wood. Tracheids rather uniform in very irregular rows. Medullary rays broad, prominent, 1 cell wide, distant 1-12, more rarely 20, rows of tracheids.

*Radial.* Ray cells straight or rarely contracted at the ends, somewhat resinous, equal to about 4 spring tracheids; the upper and lower walls thin, rather uniform, rarely pitted; the terminal walls very thin, straight or curved, and not pitted; the lateral walls with large, oval, narrowly bordered pits 2-6 per tracheid, the round or broadly oblong orifice either parallel with or diagonal to the cell axis. Bordered pits conspicuously in 1-2 rows, elliptical. Pits on the tangential walls of the summer wood numerous, small, the orifice broadly trumpet-shaped or bell-shaped; the pits on the tangential walls of the spring wood large, sometimes rather abundant. Resin cells rather numerous, 30-40  $\mu$  wide, 175-480  $\mu$  long.

*Tangential.* Rays medium to high, often more or less 2-seriate; the cells very large and broadly oval, those in the center commonly conspicuously squarish.

Wood very durable in contact with the soil and of great economic value. Trees 61-92 m. in height and 2.40-7 m. in diameter.

Relative specific gravity . . . . .	0.4208
Approximate relative fuel value . . . . .	42.02
Coefficient of elasticity in kilograms on millimeters . . . . .	676.
Ultimate transverse strength in kilograms . . . . .	255.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6656.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1242.
(Sargent)	

From the northern borders of California southward through the coast ranges to near the southern boundary of Monterey County (Sargent).

## 2. *S. gigantea*, Decaisne

### *Big Tree*

*Transverse.* Summer wood very thin, of 2-6 tracheids, the transition to the spring wood usually abrupt. Spring tracheids large, open, thin-walled, uniform, squarish, in regular rows. Resin cells not very numerous, but large and prominent, scattering. Medullary rays not very prominent, rather numerous, 1 cell wide; distant 2-14, rarely 25, rows of tracheids.

*Radial.* Ray cells usually somewhat contracted at the ends, equal to 6-8 spring tracheids, chiefly resinous throughout; the upper and lower walls thin and entire or distantly pitted, unequal; the terminal walls thin, straight or curved, not pitted or locally thickened; the lateral walls with oval and commonly narrowly bordered pits, the broadly oblong orifice equal to the outer limits of the pit and chiefly parallel to the cell axis, 1-2, or more rarely 3-4, per tracheid. Bordered pits in one or two rows, elliptical, the orifice large, elliptical. Pits on the tangential walls of the summer wood prominent and frequent; on the tangential walls of the spring wood prominent but rare. Resin cells few, about 20  $\mu$  wide and 140-325  $\mu$  long, chiefly about 250  $\mu$ .

*Tangential.* Rays chiefly low to medium, the large cells broadly oval or round, thin-walled.

A light, soft wood remarkable for its durability in the soil. The tree is the largest produced by American forests, attaining a height of 79-119 m. and a diameter of 6-11 m.

Relative specific gravity . . . . .	0.2882
Approximate relative fuel value . . . . .	28.67
Coefficient of elasticity in kilograms on millimeters . . . . .	451.
Ultimate transverse strength in kilograms . . . . .	196.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6210.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1091.

(Sargent)

Western slopes of the Sierra Nevada Mountains, California, from Placer County south to Deer Creek on the southern borders of Tulare County (Sargent).

### 3. \* \* *S. Langedorffii* (Brongn), Heer.

*Transverse.* Growth rings medium, strongly defined. Tracheids of the spring wood squarish, large,  $52 \times 52 \mu$ , the walls  $14 \mu$  thick. Summer wood of 3-6 tracheids in thickness, the transition from the spring wood rather abrupt. Resin cells rather numerous throughout the growth ring and scattering. Resin passages usually absent, but occasionally appearing in a rudimentary form on the outer face of the summer wood.

*Radial.* Medullary rays devoid of tracheids; the parenchyma cells equal to about 4 tracheids, somewhat constricted at the ends; the upper and lower walls thin and entire; the terminal walls not pitted, straight or curved; the lateral walls with no recognizable structural details.

*Tangential.* Medullary rays 1-seriate or rarely 2-seriate in part, the oval or round cells about  $31.5 \mu$  broad.

This very widely distributed and well-known Cretaceous and Tertiary plant, which is chiefly represented by foliage and fruit, is apparently represented also by the woody stem in the Lignite Tertiary of the Porcupine Creek and Great Valley groups in Saskatchewan. Reference of the wood to this species is, however, made provisionally, as the evidence is not such as to warrant an absolute decision. The occurrence of the genus in this locality, however, indicates that it at one time occupied the present prairie region in preglacial times, and that its recession to its present narrow limits probably occurred as the result of glacial action.

### 4. \* \* *S. Burgeessii*, Penh.

*Transverse.* Growth rings chiefly narrow but variable, the rather narrow but variable summer wood dense, the transition from the spring wood abrupt. Tracheids of the spring wood large, squarish, and thin-walled. Resin canals wholly wanting. Resin cells numerous throughout the growth ring, but especially on the outer face of the summer wood; with dark, massive resin. Medullary rays chiefly 1 cell wide, occasionally broader and bearing a resin canal with large thyloses.

*Radial.* Bordered pits large, in 1-2 rows. Medullary rays often with a large resin passage bearing thyloses; the cells all of one kind; the upper and lower walls thin and much altered by decay; the lateral walls devoid of recognizable markings.

*Tangential.* Ordinary rays 1- or sometimes 2-seriate in part; the fusiform rays with large resin passages containing thyloses.

An exceedingly well-characterized species from the Eocene of the Porcupine Creek and Great Valley groups.

#### 5. \* \* *S. magnifica*, Knowlton

"Trunks often of great size, 6-10 feet in diameter, 30 feet high as now preserved, bark when present 5 or 6 inches in thickness; annual rings very distinct, 2-3 mm. broad."

"*Transverse.* In this section the structure appears beautifully preserved. The rings are rather narrow, being only 2 or 3 mm. broad, or often only 1 mm. They are very sharply demarked, even to the naked eye. Under the microscope the rings are found to consist of a band of thick-walled cells that is never more than 15 rows of cells deep and often reduced to 2 or 3 rows. The cells composing the spring and summer wood are of uniform size and inclined to hexagonal in shape. Those of the fall wood are, of course, compressed.

"The resin cells are numerous and may be readily distinguished by the dark contents. They occur mainly in the spring and summer wood.

"The medullary rays seen in this section are long, straight, and separated by usually about 3 rows of wood cells."

"*Radial.* This section is the least satisfactory of all. The wood cells show well under the microscope, but their markings are very obscure. By prolonged search it is made out that the pits are in 1 row, or sometimes 2 parallel rows. They are small, as far as can be made out, and are too obscure for satisfactory measurement.

"The rays are composed of long, unmarked cells."

"*Tangential.* This section is very satisfactory. The wood cells are long and unmarked. The resin ducts are numerous, but scattered, the cells being twice or three times as long as wide. In many cases they are filled with or contain masses of dark material, representing the resin now turned to a carbonaceous mass.

"The medullary rays are composed of 1, or in some cases of a partially double, series of 2 to about 25 superimposed cells. They are large and quite thick-walled. The average number of cells in each ray is about 12" (Knowlton).

According to Professor F. H. Knowlton, this species can hardly be distinguished from the existing *S. sempervirens*, of which he considers it to be the ancestral form.

Tertiary of the Yellowstone National Park, at Specimen Ridge, Fossil Forest at head of Crystal Creek, Fossil Forest on Cache Creek, etc. (Knowlton).



## 6. \* S. Penhallowii, Jeffrey

- "*Transverse*. Rings of growth rather narrow, with sharply marked but thin summer wood. Rings regular, or if varying in thickness, varying uniformly and without violent transitions except as the result of injury. Resin canals present in both the vertical and horizontal planes apparently only as the result of injury. The resin canals when present surrounded by resin cells, containing dark brown resin. Resin cells inconspicuous and confined to the face of the summer wood, except in the case of injury, where they may be present throughout the zone of annual growth. Tracheids of the spring wood very large and with pits on the radial walls only. Tracheids of the summer wood with tangential pits."
- "*Radial*. Rays without tracheidal cells, but with distinctly differentiated marginal cells. Lateral pits of the ray cells elliptical, bordered, larger in the marginal cells. Rows of pits single in the central cells of the ray and 2-3 seriate in the marginal cells. Medullary ray cells covering 1-4 tracheids, the central ones resiniferous, the marginal generally empty, sometimes containing large clinorhombic crystals inclosed in cysts derived from the cell walls. Marginal cells with undulating free border, deeper than central cells. End walls of the cells of the medullary rays very strongly pitted. Longitudinal walls of ray cells also pitted and rather thick. Rays contain resin canals in the case of injury, which take their origin from similar vertical canals running in the wood. Resin canals of the rays sometimes ending blindly and sometimes in a more external series of vertical canals, often extending through many annual rings, varying greatly in size and frequently occluded by thyloses. Spring tracheids generally with 2 rows of opposite pits, which often alternate in the ends."
- "*Tangential*. Rays of one kind only in uninjured parts of the wood. Fusiform rays present with linear rays in the case of injury and varying greatly in size. Fusiform rays, when present, generally with central resin canal, which is often occluded by thyloses. Linear rays varying greatly in depth. No pits on the tangential walls of the spring tracheids. Pits on the tangential walls of the summer tracheids numerous, generally not in rows" (Jeffrey).

Material but slightly silicified and showing little alteration through decay.

From a waterworn fragment of a trunk originally 6 feet or more in diameter.

Miocene(?), from Tunnel No. 1, Central Pacific Railway, at Blue Gap, Sierra Nevada Mountains (Jeffrey).

## 10. \* CUPRESSUS, TOURN. PLATES 38 AND 39

*Transverse*. Summer wood usually very thin, often barely distinguishable, the structure of the growth ring open throughout. Resin passages wholly wanting. Resin cells prominent, rather numerous in bands, scattering or even apparently wanting.

*Radial.* Rays chiefly without tracheids. Terminal walls of the ray cells thin and entire, very commonly curved, often locally thickened. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting. Ray cells chiefly broad, oval, or even transversely oval; the rays sometimes 2-seriate in part.

### SYNOPSIS OF SPECIES

#### A. \* CHAMÆCYPARIS

##### *Existing Species*

1. Pits on the tangential walls of the summer tracheids flat,  
small, obscure, or at least not prominent

Ray cells (tangential) round or oval.

Ray tracheids absent.

Tracheids more or less conspicuously rounded throughout.

Ray cells (radial) straight, sparingly resinous.

Pits on the lateral walls of the ray cells 2, in radial series, or in the marginal cells 6, per tracheid.

##### 5. *C. obtusa.*

Tracheids distinctly squarish, large, the structure open.

Pits on the lateral walls of the ray cells 2-4, rarely 8, per tracheid.

##### 2. *C. Lawsoniana.*

Pits on the lateral walls of the ray cells 2, in radial series, or 6, per tracheid.

##### 3. *C. pisifera.*

Ray tracheids present in the low rays.

Tracheids distinctly squarish, or again rounded and thick-walled, the structure variable, either open or somewhat dense.

Pits on the lateral walls of the ray cells 1-4 per tracheid.

Tracheids (transverse) commonly in very irregular rows.

##### 4. *C. nootkatensis.*

Ray cells (tangential) narrow, oblong, more rarely oval.

Tracheids distinctly squarish, in regular rows, the structure open.

Pits on the lateral walls of the ray cells 1-2, or in the marginal cells and low rays upwards of 6, per tracheid.

##### 1. *C. thyoides.*

#### B. CUPRESSUS

##### *Existing Species*

2. Pits on the tangential walls of the summer tracheids chiefly  
large and open

Ray cells (tangential) round or oval, more rarely transversely oval.

Tracheids more or less conspicuously rounded throughout.

Ray cells (radial) somewhat contracted at the ends, strongly resinous.

Pits on the lateral walls of the ray cells 1-2, rarely 4, per tracheid.

6. *C. macrocarpa*.

Tracheids barely if at all rounded.

Ray cells (radial) contracted at the ends, more or less resinous.

Pits on the lateral walls of the ray cells 1-2, rarely 3, per tracheid.

8. *C. Macnabiana*.

Ray cells (tangential) chiefly transversely oval.

Tracheids more or less rounded throughout.

Ray cells (radial) somewhat contracted at the ends, barely resinous.

Pits on the lateral walls of the ray cells 1-2, more rarely 4, per tracheid.

7. *C. arizonica*.

Tracheids squarish, the structure open throughout.

Ray cells (radial) strongly fusiform, generally resinous.

Pits on the lateral walls of the ray cells 1-2 per tracheid.

9. *C. Goveniana*.

C. \* \* CUPRESSOXYLON (*Cupressinoxylon*)

*Extinct Species*

Tracheids of the spring wood distinctly rounded.

Bordered pits obliterated by decay.

Medullary rays (tangential) 1-3 seriate, the round, thin-walled cells 47  $\mu$  broad.

10. *C. cheyennense*.

Bordered pits in 1 row, distant, round.

Pits on the lateral walls of the ray cells 1-2, chiefly 2, per tracheid.

Rays (tangential) numerous, the variable cells chiefly broad, oval, or round, sometimes transversely oval.

11. *C. macrocarpoides*.

Bordered pits large, in 1 row, or often in pairs, and in larger tracheids becoming more or less 2-rowed.

Pits on the lateral walls of the ray cells 1-2 per tracheid.

Medullary rays (tangential) 1-seriate, the round cells 19  $\mu$  broad.

12. *C. comanchense*.

Tracheids of the spring wood squarish-hexagonal.

Bordered pits round, distant, in 1 row.

13. *C. pulchellum*.

14. *C. arkansanum*.

Bordered pits large, in 1 row, often in pairs, the latter sometimes so approximated as to make the pits more or less 2-rowed.

Pits on the lateral walls of the ray cells 1-2, in vertical series, or in marginal cells and low rays 4, per tracheid.

15. *C. Dawsoni*.

Pits on the lateral walls of the ray cells obliterated.

16. *C. Wardi*.

Pits on the lateral walls of the ray cells minute, round.

Medullary rays (tangential) small, the cells small, oblong,

15-17 x 10  $\mu$ .

17. *C. columbianum*.

Bordered pits conspicuously in 2 rows.

Pits on the lateral walls of the ray cells obliterated.

Growth rings obscure.

18. *C. elongatum*.

Growth rings sharply defined.

Tracheids of the earlier spring wood very large and thin-walled.

19. *C. glasgowi*.

Bordered pits in 2, or sometimes 3, rows.

Pits on the lateral walls of the ray cells with large, oval pits 1-3 per tracheid.

20. *C. McGeei*.

Pits on the lateral walls of the ray cells 3 per tracheid.

21. *C. Calli*.

## A. CHAMÆCYPARIS

### 1. \* *C. thyoides*, Linn.

#### *White Cedar*

*Transverse.* Growth rings thin, variable, the structure open throughout.

The summer wood chiefly thin, of 2-6 tracheids, the transition to the spring wood rather abrupt, or sometimes thicker and not clearly separable from the spring wood. Spring tracheids large, conspicuously squarish, uniform, in regular rows, in small stems and branches often much elongated radially, the walls not very thin. Resin cells widely scattering and often apparently wanting; when in bands, often giving the appearance of secondary growth rings, chiefly in or near the summer wood. Medullary rays not very prominent or resinous, 1 cell wide, distant 2-12 tracheids.

*Radial.* Ray tracheids chiefly narrow, very unequal, often high, sometimes present, then rather abundant and composing the entire ray when of 1 or 2 cells only, usually absent from the higher rays. Medullary rays contracted at the ends; the upper and lower walls medium to thick, unequal, frequently pitted or again entire or distantly pitted; the terminal walls thin, often curved and locally thickened; the lateral walls with round or oval pits, the orifice lenticular, 1-2, or in the marginal cells and low rays, 6, per tracheid. Pits on the tangential walls of the summer tracheids very small and often obscure. Bordered pits round or elliptical in 1 row, or in radially broad tracheids in 2 rows. Resin cells not numerous, 20-25  $\mu$  wide, 150-175  $\mu$  long.

*Tangential.* Rays medium, wholly 1-seriate; the cells narrow, oblong.

Wood very light and soft, but very durable in the soil.

Relative specific gravity . . . . .	0.3322
Approximate relative fuel value . . . . .	33.12
Coefficient of elasticity in kilograms on millimeters . . . . .	404.
Ultimate transverse strength in kilograms . . . . .	194.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4149.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1074.
(Sargent)	

Cape Breton Island and near Halifax (Macoun); southern Maine, southward along the coast to Florida, thence westward along the Gulf coast to Pearl River, Mississippi (Sargent).

The Pleistocene deposits of the Don Valley, Toronto. Material not petrified, but often showing the effects of advanced decay.

## 2. *C. Lawsoniana*, A. Murr.

*Port Orford Cedar. Oregon Cedar. White Cedar. Lawson's Cypress.*  
*Ginger Pine*

*Transverse.* Growth rings very narrow, variable, the structure very open throughout. Summer wood very thin, of 1-5 tracheids, sometimes double and then upwards of 14 tracheids, the transition to the spring wood gradual. Spring tracheids very large, squarish-hexagonal, thin-walled, in very regular rows, uniform. Resin cells prominent, large, usually widely scattering and not numerous, or again numerous within narrow zones in the summer wood. Medullary rays resinous, rather prominent and numerous, 1 cell wide, distant 1-9 or 12 tracheids.

*Radial.* Ray tracheids wholly wanting. The straight or somewhat contracted ray cells rather resinous, equal to 3-12 spring tracheids; the upper and lower walls variable, often strongly thickened toward the ends of the cells, not obviously pitted; the terminal walls thickish, chiefly straight, not pitted or locally thickened; the lateral walls with small bordered pits with a narrow orifice, 1-4, or more rarely upwards of 8, per tracheid and chiefly in vertical rows. Bordered pits in 1 row, sometimes in 2 rows, round. Pits on the tangential walls of the

summer tracheids small, rarely large, not numerous. Resin cells not numerous, 20–25  $\mu$  wide, 150–200  $\mu$  long, chiefly about 175  $\mu$ .

*Tangential.* Rays medium, wholly 1-seriate; the cells broadly oblong or oval, sometimes round, the walls thick.

A light, hard, and strong wood which is very durable in the soil.

Relative specific gravity . . . . .	0.4621
Approximate relative fuel value . . . . .	46.16
Coefficient of elasticity in kilograms on millimeters . . . . .	1217.
Ultimate transverse strength in kilograms . . . . .	379.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7435.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1317.

(Sargent)

Oregon, not more than thirty miles from the coast; valley of the upper Sacramento River, California (Sargent).

### 3. *C. pisifera*, Sieb. et Zucc.

*Jap. = Sawara*

*Transverse.* Growth rings narrow, uniform; the usually dense and very narrow summer wood of 3–5 tracheids, the transition to the spring wood somewhat abrupt; the spring wood open, the large, squarish-hexagonal tracheids in very regular rows, uniform, rather thin-walled. Resin cells few, dark, and prominent, zonate in the summer wood. Medullary rays not prominent, 1 cell wide, narrow, distant 2–17 tracheids.

*Radial.* Rays devoid of tracheids, nonresinous, the cells contracted at the ends, equal to 5–6 spring tracheids; the upper and lower walls thin, rather unequal, not obviously pitted; the terminal walls thin, chiefly curved, not pitted or locally thickened; the lateral walls with oval, bordered pits, chiefly 2 per tracheid in radial series, or in the marginal cells and low rays smaller and upwards of 6 per tracheid. Bordered pits elliptical, large, rather numerous in 1 row or sometimes in pairs. Pits on the tangential walls of the summer tracheids rather few, small, flat, and inconspicuous. Resin cells few in the summer wood, 12.5–20  $\mu$  wide, 170–250  $\mu$  long.

*Tangential.* Rays low to medium, narrow, nonresinous; the cells rather variable from oblong to oval or round, chiefly rather oblong, rarely if ever in pairs.

### 4. *C. nootkatensis*, Lam.

*Yellow Cypress. Sitka Cypress*

*Transverse.* Growth rings unequal. Summer wood very thin, of 2–6 tracheids, the transition to the spring wood gradual. Spring tracheids chiefly large, but very variable and often in irregular rows, squarish. Resin cells prominent and rather numerous, either scattering or compressed into narrow bands in both the spring and summer wood. Medullary rays resinous, prominent, 1 cell wide, distant about 2–17 tracheids.

*Radial.* Ray tracheids chiefly short and broad; chiefly or wholly confined to rays 1 or 2 cells high, then constituting the entire ray, not very numerous. Ray cells somewhat resinous, more or less conspicuously contracted at the ends, equal to 4-9 spring tracheids; the upper and lower walls thick and entire or distantly pitted; the terminal walls thin and locally thickened; the lateral walls with rather small pits with a lenticular orifice often parallel with the cell axis, 1-4 per tracheid. Bordered pits round or elliptical in 1 row, somewhat distant; the round orifice often very variable, much enlarged, eccentric, irregular in outline or even wanting, the pits then presenting a variable aspect which at once serves to define the species. Pits on the tangential walls of the summer tracheids few, often obscure. Resin cells few, about 20  $\mu$  wide and 100-175  $\mu$  long, rarely upwards of 270  $\mu$ .

*Tangential.* Rays low, narrow, and 1-seriate, sometimes 2-seriate in part; the cells narrowly elliptical or broadly oval, sometimes transversely oval or oblong, much enlarged.

This is the most variable species of *Cupressus*, and it is chiefly remarkable for the variable character of the summer wood, the irregular disposition of the tracheids (transverse), the often very numerous resin cells, and the peculiarly imperfect bordered pits which at once separate it from all other species. It may show deviation from the normal in (1) the absence of resin cells; (2) the form of the tracheids, which are sometimes round with thick walls, even in the same section, thus giving rise to (3) a variable structure of the wood which is in some rings rather dense throughout.

A large tree of great economic importance with a height of 30-38 m. and a diameter of 1.20-1.80 m. Wood light, hard, and very durable.

Relative specific gravity . . . . .	0.4782
Approximate relative fuel value . . . . .	47.66
Coefficient of elasticity in kilograms on millimeters . . . . .	1029.
Ultimate transverse strength in kilograms . . . . .	342.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7281.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1618.

(Sargent)

Interior of Vancouver Island; British Columbia, near the coast, where it reaches sea level in the northern portions, and thence to Alaska (Macoun); southward through the Cascade Mountains of Washington and Oregon, where it is seldom found below an elevation of 5000 feet (Sargent).

##### 5. *C. obtusa*, Sieb. et Zucc.

*Jap.* = *Hinoki*

*Transverse.* Growth rings broad. Summer wood chiefly rather thin, sometimes double, rather open but passing very gradually into the broad spring wood from which it is not clearly separable. Tracheids of the spring wood round-hexagonal, thickish-walled, not very large, the

structure not very open. Resin cells prominent, dark, not very large or numerous, rather scattering or again zonate in both spring and summer woods. Medullary rays not prominent or numerous, rather narrow and 1 cell wide, distant 1-23 tracheids.

*Radial.* Medullary rays devoid of tracheids, sparingly resinous, the cells straight and equal to 5-10 spring tracheids; the upper and lower walls thickish, sinuately unequal, not obviously pitted; the terminal walls thin, curved or straight, not pitted or locally thickened; the lateral walls with oval, bordered pits, chiefly 1, or in the marginal cells 2, per tracheid, the orifice lenticular-oblong. Bordered pits round or elliptical, rather distant in 1 row, usually less than one half the diameter of the tracheid. Pits on the tangential walls of the summer tracheids not very numerous, small, flat, obscure. Resin cells few, 15-25  $\mu$  wide, 150-210  $\mu$  long, chiefly about 150  $\mu$ .

*Tangential.* Rays medium, narrow; the uniformly oval, nonresinous cells rarely if ever in pairs.

## B. CUPRESSUS

### 6. *C. macrocarpa*, Gordon

#### *Monterey Cypress*

*Transverse.* Growth rings usually broad. Summer wood very thin, of 6-8 tracheids, and passing gradually into the spring wood from which it is not always clearly separable. Spring wood very broad, the tracheids uniform, rather large, rounded-hexagonal, the walls rather thick. Resin cells prominent and widely scattering or somewhat zonate in the summer wood. Medullary rays prominent, resinous, broad, 1 cell wide, distant 2-12, rarely 33, tracheids.

*Radial.* Rays devoid of tracheids and resinous throughout. Cells more or less contracted at the ends, equal to 4-6 spring tracheids; the upper and lower walls variable and not obviously pitted; the terminal walls thin, often curved, locally thickened; the lateral walls with rather large bordered pits with large, lenticular, or oblong orifices, 1-2, or in the low rays 4, per tracheid. Bordered pits round or elliptical, sometimes in pairs. Pits on the tangential walls of the summer tracheids numerous, large, and open. Resin cells not numerous, 20-25  $\mu$  wide, 40-65  $\mu$  long, chiefly about 50  $\mu$ .

*Tangential.* Rays medium, sometimes 2-seriate in part, the cells broadly often transversely oval, thick-walled.

This species is usually recognized by the very large, bordered pits on the tangential walls of the summer tracheids. In transverse section the summer wood commonly presents somewhat strong variations in specimens from different individuals.

Wood heavy, hard, strong, and very durable. Trees upward of 21 m. in height and 1.80 m. in diameter.

Relative specific gravity . . . . . 0.6261  
(Sargent)

California (Sargent).



7. *C. arizonica*, Greene*Cypress*

*Transverse.* Growth rings medium, rather uniform. Summer wood very thin, upwards of 6 tracheids, and passing very gradually into the spring wood. The very broad spring wood somewhat open, the very variable tracheids chiefly squarish-hexagonal, the walls not thin. Resin cells numerous and prominent, narrowly zonate in both the spring and summer woods, sometimes in groups of larger and thicker-walled cells, showing a tendency to the formation of resin canals. Medullary rays rather prominent, somewhat resinous, rather numerous and broad, 1 cell wide, distant 2-10 tracheids.

*Radial.* Rays devoid of tracheids and sparingly resinous, the cells conspicuously contracted at the ends, equal to about 6-9 spring tracheids; the terminal walls chiefly straight, sparingly and locally thickened; the upper and lower walls medium to thick, not obviously pitted; the lateral walls with round or oval pits 1-2, or in the marginal cells 4, per tracheid. Bordered pits round or elliptical, rather numerous, in 1 row. Pits on the tangential walls of the summer tracheids rather numerous and large, open. Resin cells not numerous, 15-20  $\mu$  wide, 120-250  $\mu$  long, chiefly about 200  $\mu$ ; sometimes in multiple series of much broader, very variable, often isodiametric and thick-walled cells, showing a strong tendency to the formation of resin canals.

*Tangential.* Rays medium, the cells broad, more or less resinous, transversely oval, or in the low rays vertically oval.

Wood soft, light, and coarse grained.

Relative specific gravity . . . . . 0.4843  
(Sargent)

San Francisco Mountains of New Mexico and Arizona, where the tree forms extensive forests on the northern slopes of the mountains at elevations of 5000-8000 feet; Santa Catalina and Santa Rita mountains of Arizona; on the Sierra Madre and Guadeloupe Island, Mexico (Sargent).

8. *C. Macnabiana*, A. Murr.*Cypress*

*Transverse.* Growth rings medium, uniform. Summer wood very thin, of about 3-5 tracheids, open, the transition to the spring wood gradual. The broad spring wood rather open, the tracheids conspicuously hexagonal, rather uniform, the walls medium. Resin cells prominent, not numerous, widely scattering throughout the growth ring. Medullary rays prominent, somewhat resinous, 1 cell wide, distant 1-10, rarely 14, tracheids.

*Radial.* Rays wholly devoid of tracheids, more or less resinous throughout, individual cells often strongly so. The cells somewhat contracted at the ends, equal to 4-5 spring tracheids; the upper and lower walls medium, unequal, entire, or sparingly pitted; the terminal walls thin and

chiefly straight, locally thickened; the lateral walls with oval or round bordered pits, orifice lenticular, 1-2, or in the marginal cells rarely 3, per tracheid. Bordered pits rather numerous in 1 row, elliptical, the orifice large. Pits on the tangential walls of the summer tracheids rather numerous and large, the orifice bell-shaped, not very open. Resin cells not numerous, 12.5-25 or sometimes 35  $\mu$  broad, 210-310  $\mu$  long, chiefly about 250  $\mu$ .

*Tangential.* Rays low, the cells broad, oval, or round, often resinous.

A small tree of the mountains of Lake County, California (Sargent).

### 9. *C. Goveniana*, Gordon

#### *Cypress*

*Transverse.* Growth rings variable. Summer wood very thin, of 2-6 tracheids; the transition to the spring wood gradual. Spring wood very open, the tracheids large and squarish, in regular rows, rather uniform and thin-walled. Resin cells abundant and prominent, in narrow but well-defined zones, sometimes forming rather extended radial series, 1 to 3 cells wide, of broader and thicker-walled cells. Medullary rays rather numerous but not very resinous or prominent, 1 cell wide, distant 2-8, rarely 15, tracheids.

*Radial.* Rays devoid of tracheids, more or less resinous. Ray cells conspicuously narrower at the ends, equal to 3-8 spring tracheids, becoming shorter in the summer wood; the upper and lower walls medium, entire or distantly pitted; the terminal walls thin, often locally thickened; the lateral walls with round or oval pits having large, round or oval openings, 1-2, or in the marginal cells 4, per tracheid. Bordered pits elliptical, sometimes round in 1 row, becoming much more distant and smaller toward the summer wood. Pits on the tangential walls of the summer tracheids rather numerous, prominent, chiefly large and open. Resin cells rather abundant, 10-20  $\mu$  wide, 185-375  $\mu$  long, chiefly about 225  $\mu$ ; sometimes in radially wide, multiple series of broad and short, thick-walled cells.

*Tangential.* Rays low and broad, sometimes 2-seriate in part; the cells thick-walled, chiefly transversely oval.

This species is largely distinguished by the smaller pits on the lateral walls of the strongly contracted ray cells, and by the transversely oval ray cells as shown in tangential section.

A small tree furnishing a light, soft wood.

Relative specific gravity . . . . .	0.4689
Approximate relative fuel value . . . . .	46.68
Coefficient of elasticity in kilograms on millimeters . . . . .	499.
Ultimate transverse strength in kilograms . . . . .	230.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5742.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2852.
(Sargent)	

Humboldt County, California, south along the coast, and through the coast ranges into southern California (Sargent).

## C. \*\* CUPRESSOXYLON (Cupressinoxylon)

*Extinct Species Only*

## 10. \*\* C. cheyennense, Penh.

*Transverse.* Tracheids in regular, radial rows, rather uniform, roundish, about  $62 \times 62 \mu$  broad; the walls  $15.5 \mu$  thick. Resin passages and special resin cells wanting. Growth rings apparent, very broad; in a radial extent of 20 mm., 2 growth rings of an equal thickness of 10 mm. are represented. The summer wood conspicuous, about 3-4 cells thick, the tracheids about  $29 \times 38 \mu$  broad, the tangential walls about  $15.5 \mu$  thick.

*Radial.* Ray cells all of one kind, straight; the upper and lower walls thin and not pitted; the terminal walls thin and not pitted, straight or curved; the lateral walls showing no structure which has been obliterated by decay; the cells 3-5 tracheids long.

*Tangential.* Rays numerous, medium, 1-3 seriate; the cells round, thin-walled,  $47 \mu$  broad.

Material silicified. Specimens represented by small portions of stem.

From the Cheyenne Formation (Comanche Cretaceous), east of Stokes Hill, Kiowa and Baker County line, Kansas (Prosser).

## 11. \*\* C. macrocarpoides, Penh.

*Transverse.* Growth rings rather broad. Tracheids of the spring wood round but thin-walled through the obvious effects of decay; rather uniform in regular rows, and passing gradually into the rather thin but conspicuous summer wood. Resin passages wholly wanting. Resin cells not recognizable. Medullary rays prominent, often 2 cells wide, distant 1-6 rows of tracheids.

*Radial.* Medullary rays wholly devoid of tracheids. Ray cells more or less conspicuously contracted at the ends, equal to about 6 spring tracheids; the upper and lower walls rather thin and sparingly pitted; the terminal walls chiefly straight, sometimes curved, not pitted or obviously thickened locally; the lateral walls with oval or round pits, 1-2, chiefly 2, per tracheid. Bordered pits in 1 row, chiefly distant, round. Pits on the tangential walls of the summer wood not recognizable. Resin cells present on the outer face of the summer wood (?),  $30 \mu$  wide and  $125 \mu$  long.

*Tangential.* Fusiform rays wholly wanting. Ordinary rays numerous, low to high, often more or less 2-seriate, rarely 3-seriate in part; the cells variable, chiefly broad, oval or round, or sometimes transversely oval. Resin cells rather numerous, usually very long, the resin scattering in small globules.

Material silicified.

Cretaceous near Medicine Hat, Alberta; Tertiary of Kettle River, near Midway, British Columbia.

12. \*\* *C. comanchense*, Penh.¹

*Transverse.* Tracheids in regular, radial rows, rounded, very uniform,  $44 \times 44 \mu$  broad, the walls  $12.5 \mu$  thick. Growth rings prominent, about 10 in a radial extent of 22 mm.; the summer wood thin, composed of 2-4 rows of tracheids, the latter about  $22 \mu$  wide, the walls  $12.5 \mu$  thick. Resin passages and resin cells wholly wanting. Worm burrows are frequent and show copious exudation of resin, which has often preserved the adjacent structure from decay.

*Radial.* Ray cells of one kind only, straight; the upper and lower walls thin and not pitted; the terminal walls thin, not pitted, chiefly curved; the lateral walls with oval, bordered pits, about 1-2 per tracheid, the oblong or broadly lenticular orifice nearly as long as the pit; the cells equal to about 4 tracheids. Bordered pits round, large,  $19 \mu$  broad; in 1 or sometimes 2 rows, the orifice round.

*Tangential.* Rays 1-seriate, the cells thin-walled, round,  $19 \mu$  broad.

Material silicified. Specimens represented by small fragments of a stem. Comanche Cretaceous (?) northwest of Ashland, Clark County, Kansas (Prosser).

13. \*\* *C. pulchellum*, Knowlton

"*Transverse.* The pith is well preserved and consists, when viewed under the microscope, of numerous large, rather thick-walled cells with an elliptic or nearly circular outline. The larger cells, which have a diameter of .05-.08 mm., occupy the center, from which they decrease in size and pass more or less gradually into the medullary rays. The rays are very numerous and pass in nearly a straight line to the circumference. No trace of bark remains. The tracheids are arranged with great regularity in radial rows, and are remarkable for their small size, particularly where they are in contact with the pith. As the medullary rays diverge, new layers of tracheids are intercalated to fill up the space. The line of demarcation between the annual layers is generally well defined, the fall wood consisting of 5-8 compressed cells in each radial row. The spring wood consists of much larger cells, which have a diameter of .025-.035 mm. These cells are more nearly hexagonal than the others, and, decreasing gradually in size, pass into the next ring of fall wood.

"*Radial.* In this section the tracheids are seen to be long and provided with a single longitudinal row of bordered pits, which have an average outer diameter of .017-.021 mm. The inner circle of the pits is rather small, with a diameter of .005-.006 mm. The medullary rays are cut up into comparatively short cells, each one covering the space of five or six of the tracheids; markings seem to be absent from the walls of the rays, but the real state of affairs may be masked by the petrifying material, which has evidently somewhat disorganized the original structure. The resin ducts (cells) are numerous. These consist of a chain of short, regular cells, which are slightly constricted at the ends. The individual cells are .08-.15 mm. in length, and are usually filled with minute globules of darker matter.

"*Tangential*. The medullary rays are very abundant. They are always simple and consist of a single layer, which ranges from 1 to 15 cells in height, the average being about 7 or 8. The tracheids do not show bordered pits on the tangential walls, a fact of considerable importance" (Knowlton).

Remains silicified.

From the Potomac Formation at Spring Hill, Virginia (Knowlton).

#### 14. \* \* *C. arkansanum*, Knowlton

"*Transverse*. The annual ring is either entirely absent or so obscured by the mass of crushed cells as to be indistinguishable. In a single, exceptionally well-preserved spot the tracheids are seen to be arranged in nearly uniform radial rows, there being generally about 3 or 4 rows between 2 medullary rays. The rays are abundant and consist of a single cell.

"*Radial*. The tracheids are rather thick-walled and provided with a single row of pits. The pits are rather distant, the outer circle having a diameter of .011-.0145 mm., and the inner a diameter of .0028-.0048 mm. The medullary rays are abundant, and usually only a single series thick, although a few may be found with 2 series of cells in the center.

"*Tangential*. The material is not sufficiently well preserved to determine the medullary rays satisfactorily" (Knowlton).

Remains silicified.

From the Tertiary deposits (Orange sands) of Poinsett County, Arkansas (Knowlton).

#### 15. \* \* *C. Dawsoni*, Penh.

*Transverse*. Growth rings variable, chiefly medium to broad. Tracheids of the spring wood large, thin-walled, conspicuously squarish, and passing gradually into the usually thin but rather prominent summer wood, which may occasionally become thicker and without definite internal demarcation. Resin passages wholly wanting. Resin cells numerous and conspicuous throughout the growth ring, often in more or less prominent, tangential row. Medullary rays prominent, resinous, 1 cell wide but rather broad, distant 2-9 rows of tracheids.

*Radial*. Medullary rays devoid of tracheids. Ray cells resinous, contracted at the ends, equal to 5-6 spring tracheids; the upper and lower walls thin and sparingly pitted; the terminal walls straight, or sometimes strongly curved, not pitted or locally thickened; the lateral walls with round or oval pits, 1-2 per tracheid in vertical series, or in marginal cells and low rays, or over very broad tracheids, becoming 4 per tracheid. Bordered pits large, in 1 row, often more or less in pairs, and so, over broad tracheids, becoming more or less 2-rowed. Resin cells numerous, 35-40  $\mu$  wide, 200  $\mu$  long.

*Tangential*. Medullary rays of one kind only and 1-seriate; the cells rarely in pairs, large, thin-walled, oval or oblong, usually broad, and often becoming transversely oval in all except the terminal cells. Resin cells as in the radial section.

Material silicified.

Eocene of the Great Valley and Porcupine Creek groups, the province of Saskatchewan; Cretaceous of the south Saskatchewan near Medicine Hat, Alberta.

#### 16. *C. Wardi*, Knowlton

"*Transverse*. Material too fragmentary and too poorly preserved to show the annual rings to the naked eye, but they are apparent under the microscope. The fall wood consists of 3-6 or 3-8 compressed cells in radial rows. The spring wood contains some very large cells, with a diameter in some instances of .062 mm. The number of cells in each row of tracheids varies according to the width of the annual ring, there being frequently as much as 100. Large intercellular spaces occur, especially where additional rows of tracheids have been introduced.

"*Radial*. Tracheids provided in 1 row, or, in some instances, with 2 longitudinal rows of bordered pits. They occupy the center of the cell, and are in close relations, almost touching in some cases. The larger have a diameter of .02 mm., and the smaller a diameter of .015 mm. The medullary rays consist of typical parenchymatous tissue. The individual cells are short, covering a width of 4-8 tracheids. Pits on the lateral walls of the rays not observable, possibly due to the poor state of preservation. The resin ducts (cells) are not very numerous. They are of nearly the same size and shape as the tracheids, and in fact look very much like tracheids with transverse partitions. They are almost always empty.

"*Tangential*. The tracheids are not provided with pits on the tangential walls, or at least none have been detected. The medullary rays in many cases are 2 cells broad, and, as indicated, 1-35 cells high. The individual cells of the rays have a diameter of .017-.03 mm." (Knowlton).

Material silicified. Specimens represented by small fragments only.

From the Potomac Formation on the line of the Baltimore and Ohio Railroad, between Montello and Rives Station, D.C. (Knowlton).

#### 17. *C. columbianum*, Knowlton

"*Transverse*. The annual ring is very indistinct, although not entirely absent, as slight traces of it are to be observed among a mass of crushed cells. Tracheids in very regular, radial rows, and remarkable for their nearly uniform size and thick walls. The larger cells are about .05 mm. in diameter, the smaller .03-.04 mm. in diameter. The medullary rays are not abundant and appear very narrow.

"*Radial*. The tracheids are thick-walled and covered with 1, or rarely 2, rows of bordered pits, which are rather small. The larger pits have a diameter of .015 mm. and the smaller a diameter of only .01 mm. The rays consist of long cells, in some cases provided with minute, round punctations. The resin ducts (cells) are numerous. In most cases they consist of a regular chain of short, constricted cells. In some cases they contain small globules of resinous matter.

"*Tangential*. The medullary rays have very small cells which have a long diameter of .015-.017 mm. and a short diameter of only .01 mm. The walls of the tracheids are so thick and the rays so small that the walls between which they appear are but slightly bulged. The tracheids do not exhibit pits on the tangential walls" (Knowlton).

Remains silicified. The specimen is represented by numerous fragments of stem, upwards of 25 cm. in length.

The Potomac Formation of Dutch Gap and Nebasco Creek, Virginia (Knowlton).

#### 18. *C. elongatum*, Knowlton

"*Transverse*. Annual rings apparent to the naked eye, but faint,  $\frac{1}{2}$ -6 mm. broad. The layer of the fall wood is narrow, consisting of only 6-10 rows of flattened and thick-walled cells. The cells of the spring and summer wood are much larger and rectangular in outline. Their radial diameter is as great as .105 mm. in some cases, while the tangential diameter is only .035-.04 mm. The average size is about .07 mm. in long, and .03-.05 mm. in short, diameter. The medullary rays are observed to be numerous. The largest cells are in contact with the medullary rays.

"*Radial*. The wood cells or tracheids appear broad and thick-walled, and to be provided with 2 rows of very large pits which nearly touch in the center, and are in contact with the walls on the outside. The diameter of the outer circle is .02 mm., that of the inner circle .004-.006 mm. They are rarely in a single row when they occupy the center of the cell. The resin ducts consist of a chain of short cells, the contents of which are not preserved. Medullary rays abundant; individual cells long, covering the width of 6 or 8 tracheids; thin-walled. They seem not to have been provided with pits or markings.

"*Tangential*. Medullary rays in a single series, and rarely of 1-44 superimposed cells. It is not common to find rays with less than 5 cells or more than 30, the average being about 10-25. No pits on the walls of the tracheids" (Knowlton).

Remains silicified. Specimen represented by a log about 30 feet long in a clay soil.

From the Laramie of Tiger Buttes, Dawson County, Montana (Knowlton).

#### 19. *C. glasgowi*, Knowlton

"*Transverse*. Annual rings very sharply marked, 3-4 $\frac{1}{2}$  mm. broad. Under the microscope the cells are shown to be arranged in strict radial rows, and in the band of summer wood consist of a layer of 18-30 cells more or less completely lignified. In the outer layers of this lignified band of fall wood the lumen of the cells is reduced to a minimum. The lumen is in the form of an ellipse, of which the long diameter is less than .01 mm. and the short diameter about .005 mm. In the immediately following layer of spring wood the cells are very large and thin-walled, measuring .08 mm. in long, and

.05 mm. in short, diameter. In the summer wood the cells become smaller and more nearly hexagonal in outline, and pass abruptly into the band of fall wood.

"*Radial*. In this section, as in the transverse, the demarcation between fall and spring wood is very clearly marked. The walls of the cells in the spring and summer wood are the only ones provided with bordered pits, and in these they seem not to have been very abundant, or at least are not preserved in a manner capable of demonstration. These pits are usually arranged in 2 parallel rows, although in some cases there is but 1 row, when it occupies the center of the cell. The pits are large, and when in 2 rows take up nearly the entire width of the cell. The diameter of the outer circle is in extreme cases fully .025 mm., the average being about .02 mm.; the diameter of the inner circle is only .0025-.004 mm. The medullary rays are observed to be numerous, with the individual cells very long. The latter are not, however, very high, and they are thin-walled. The pits on the lateral walls are not recognizable. The resin ducts are moderately numerous. They are composed of a chain of short, thin-walled cells .15-.25 mm. in length, and are partially filled with a dark mass representing the resin.

"*Tangential*. In this section the medullary rays are observed to be composed of a single series of cells which ranges from 3 to 30 in number. It is rare, however, to find them with as few as 3 or as many as 30 cells, the average number being from 8 to 15. Bordered pits have not been observed in this section" (Knowlton).

Material silicified.

Cretaceous (?) of Emmet County, Iowa (Knowlton).

## 20. C. McGeei, Knowlton

"*Transverse*. The tracheids are arranged in strictly radial rows. The annual ring is broad, consisting in some cases of as many as 50 or 60 of the larger, and 10-16 of the smaller, thick-walled cells. The larger cells are mostly quadrangular in outline and have a diameter in some instances of .08 mm., the average being about .068 mm. The cells of the fall wood have very thick walls and are much flattened. Intercellular spaces are frequently observed, particularly where additional rows of tracheids have been intercalated. The medullary rays are moderately numerous.

"*Radial*. The large size of the tracheids is very clearly shown, and they make up the bulk of the section. The tracheids of the fall wood are, of course, much smaller, and are covered with but a single row of pits. The bordered pits are very close together on the summer wood, and are always in 2, and in some exceptionally large cells, in 3 rows. They are also very large, the outer circle having a diameter of .02-.025 mm., and the inner of .005-.008 mm. The walls of the medullary rays are marked by large, oval pores, from 1 to 3 of which occupy the width of a single wood cell. The resin ducts consist of a chain of short, small, thin-walled cells, which now contain a small quantity of granular matter, representing probably drops of resin.



The individual cells have a length of .12-.25 mm., and a diameter of about .05 mm., slightly less, it will be observed, than the tracheids among which they run.

- "*Tangential*. The medullary rays are always simple; that is, they consist of but a single row of cells, which varies from 2 to 49 cells in height. The tracheids are provided on the tangential walls with a few scattered, bordered pits. These have a diameter of .016-.021 mm." (Knowlton).

Remains silicified. Specimens represented by a trunk nearly 40 feet long and almost 2 feet in diameter.

Potomac Formation at Washington, D.C. (Knowlton).

### 21. C. Calli, Knowlton

- "*Transverse*. The annual rings are very distinct, being marked by a layer of fall wood 6-15 or more cells in thickness. These cells are very thick-walled, the lumen being reduced to a mere line. The cells of the spring wood are very large and begin abruptly at the ring, and gradually diminish in size until they reach and pass into the fall wood. The medullary rays as seen in this section are numerous and are separated by 2-4 rows of tracheids.

- "*Radial*. In the spring and summer wood the tracheids are very broad and provided with 2-3 rows of regularly and closely packed bordered pits. These pits have an average diameter of .012 mm. and an average inner diameter of .003 mm. The medullary rays are thin-walled and in some cases, at least, provided with pits, of which there are usually 3 in thickness of each tracheid. The resin tubes consist of a chain of short, rectangular cells; they are moderately numerous.

- "*Tangential*. The medullary rays are arranged in a single series of superimposed cells, which varies from 2 to 25, the ordinary number being 6-15. The tracheids are not provided with pits on the tangential walls" (Knowlton).

Remains silicified.

From the Tertiary clays of Greene County, Arkansas (Knowlton).

## 11. \* JUNIPERUS, LINN. PLATES 40 AND 41

*Transverse*. Growth rings generally narrow, often unconformable and coalescent on the narrow side; the summer wood usually thin but dense. Resin passages wholly wanting. Resin cells rather numerous, prominent, and chiefly in tangential bands, often giving rise to the appearance of secondary growth rings.

*Radial*. The numerous and often very resinous rays chiefly without tracheids. Ray cells with thin and entire or sometimes coarsely pitted terminal walls; the lateral walls with bordered pits. Bordered pits round or oval, chiefly in 1 row, generally numerous. Tracheids wholly without spirals.

*Tangential*. Fusiform rays wholly wanting. Ordinary rays 1-seriate, sometimes 2-seriate in part, the cells oval, chiefly broad.

## SYNOPSIS OF SPECIES

1. Ray cells (tangential) oval to round or transversely oval,  
resinous, conspicuously broad  
Ray cells (radial) resinous throughout.  
4. \* *J. californica*.  
Ray cells (radial) locally resinous. Rays usually higher (tangential) than  
in No. 4  
5. *J. utahensis*.
2. Rays (tangential) rather broad, the cells oval to round, chiefly  
round, sometimes in pairs, resinous  
Bordered pits (radial) numerous, usually more or less distant.  
Rays (tangential) rather high, more or less 2-seriate or the cells in  
pairs; the cells chiefly very round, rarely transversely oval.  
9. *J. pachyphlæa*.  
Rays (tangential) low, the cells rarely in pairs, round to oval, not trans-  
versely oval  
1. \* *J. virginiana*.  
Bordered pits (radial) numerous, usually crowded into compact series.  
Rays (tangential) with conspicuously and uniformly rounded cells.  
10. *J. monosperma*.
3. Ray cells (tangential) chiefly oval, the rays low, barely resinous  
Summer wood of 2-4, rarely of 10, tracheids.  
Pits on the lateral walls of the ray cells chiefly 2 per tracheid.  
11. *J. occidentalis*.  
Summer wood conspicuously thicker.  
Pits on the lateral walls of the ray cells 1-4 per tracheid.  
6. *J. sabinoides*.
4. Rays (tangential) narrow, the cells oblong to oval, chiefly oblong  
Pits on the lateral walls of the ray cells chiefly 2 per tracheid. Ray cells  
resinous.  
Terminal walls of the ray cells strongly pitted.  
Rays with narrow tracheids.  
7. *J. communis*.  
Terminal walls of the ray cells thin and not pitted.  
Rays without tracheids.  
3. *J. rigida*.  
Pits on the lateral walls of the ray cells large, 2-4 per tracheid, obscurely  
and irregularly bordered.  
2. *J. nana*.  
Pits on the lateral walls of the ray cells not very large, chiefly 4 per  
tracheid. Ray cells sparingly resinous.  
8. *J. sabina*.

1. \* *J. virginiana*, Linn.*Red Cedar. Savin*

*Transverse.* Growth rings usually broad, often double or treble. The thin summer wood rather open and passing gradually into the broad spring wood. Spring wood rather open, the tracheids variable with medium walls, in regular rows. Resin cells rather small and usually disposed in 1-2 open bands chiefly in the spring wood. Medullary rays not very prominent or resinous, rather numerous, 1 cell wide, distant 2-13 tracheids.

*Radial.* Ray cells not very resinous, equal to 5-10 spring tracheids; the upper and lower walls rather thick, unequal and remotely pitted; the terminal walls thin, straight, and entire, rarely curved or locally thickened; the lateral walls with small, chiefly bordered pits 6  $\mu$  broad, chiefly 2, more rarely 4, per tracheid, the orifice narrow, linear-oblong. Bordered pits round, in 1 row, sometimes in pairs, the orifice rather large. Pits on the tangential walls of the summer tracheids numerous, flat. Resin cells about 20  $\mu$  broad, 100-150  $\mu$  long.

*Tangential.* Rays sometimes 2-seriate in part, low; the cells small, narrowly oval to round, chiefly round, thick-walled, resinous.

A tree 20-30 m. high, with a trunk .60-1.35 m. in diameter. Wood light, soft, not strong, brittle, very close and straight grained, compact, easily worked, very durable in contact with the soil, odorous.

Relative specific gravity . . . . .	0.4926
Approximate relative fuel value . . . . .	49.11
Coefficient of elasticity in kilograms on millimeters . . .	670.
Ultimate transverse strength in kilograms . . . . .	316.
Ultimate resistance to longitudinal crushing in kilograms .	6750.
Resistance to indentation to 1.27 mm. in kilograms . . .	2376.
(Sargent)	

Nova Scotia; uncommon about Ottawa, but becoming more common westward throughout Ontario, abundant at Bay of Quinte, thence southward, crossing the St. Lawrence River midway between Montreal and Lake Ontario (Macoun); southward from New Brunswick to Tampa Bay, Florida; westward through Texas, Nebraska, Kansas, and Oklahoma to the 100th parallel, thence north to northern Michigan, Wisconsin, and Minnesota; in the Pacific region through the mountains of Colorado and British Columbia to Vancouver Island (Sargent).

Pleistocene of the Don Valley, Toronto.

Material not petrified, but remarkably well preserved in its natural state, and exhibiting the characteristic odor when cut.

2. *J. nana*, Willd.*Common Juniper*

*Transverse.* Growth rings very variable and unconformable, the tracheids very small throughout. Summer wood thin, of 3-6 tracheids, rather open, often double, the transition from the spring wood gradual. Spring wood broad, the tracheids squarish-hexagonal, not very uniform, small, the walls medium, the general density varying greatly in different rings. Medullary rays inconspicuous, 1 cell wide, distant 2-10 rows of tracheids. Resin cells numerous, prominent, distinctly zonate.

*Radial.* Rays very sparingly, if at all, resinous throughout, wholly devoid of tracheids. Ray cells variable in height, chiefly straight or becoming contracted in the summer wood, equal to 7-8 spring tracheids; the upper and lower walls thin, with broad, unequal, and usually rather distant pits; the terminal walls thin, often curved, entire or locally thickened; the lateral walls with large, very prominent, oval pits with an obscure and unequal border, 2-4, or in the summer wood 2, per tracheid. Bordered pits numerous, large, as broad as the tracheid, in 1 row. Pits on the tangential walls of the summer tracheids numerous, large, and open. Resin cells 20  $\mu$  wide, about 165  $\mu$  long.

*Tangential.* Rays rather numerous, low to medium; the cells equal, rather uniform and oblong, sometimes oval, the walls thin.

Of uncertain range in the northern parts of the continent; Lake Mistassini; the Shickshock Mountains, Gaspé; Bow River, Alberta; Rocky Mountains from Silver City westward to the summit of the Selkirks in latitude 51°; also the south and north Kootenay passes (Macoun); Labrador southward to Massachusetts and New York, thence westward to Michigan, Colorado, and Utah (Britton).

3. *J. rigida*, Sieb. et Zucc.*Jap. = Muro*

*Transverse.* Growth rings broad, the structure rather open throughout.

Summer wood very thin, of 3-4 tracheids, the transition from the spring wood rather gradual. Spring tracheids conspicuously hexagonal, rather thin-walled, uniform in regular rows. Medullary rays not very prominent or resinous, 1 cell wide, distant 2-12 rows of tracheids, more rarely 32. Resin cells prominent, usually distant in very narrow zones of occasional growth rings.

*Radial.* Rays somewhat resinous throughout, devoid of tracheids. Ray cells chiefly straight or somewhat contracted in the summer wood; the upper and lower walls medium, unequal, distinctly perforate with broad and unequal pits; the terminal walls thin, often curved, entire or locally thickened; the lateral walls with rather large, oval, narrowly bordered pits, the broadly lenticular orifice becoming oblong in the summer wood, 1-2, or in the marginal cells 4, per tracheid. Bordered pits round, somewhat distant in 1 row, not very numerous.

Pits on the tangential walls of the summer tracheids rather numerous but not very large or prominent. Resin cells few, 15  $\mu$  wide, 185–240  $\mu$  long.

*Tangential.* Rays somewhat numerous, medium; the cells chiefly equal, rather uniform, oblong, more rarely oval and broader.

#### 4. \* *J. californica*, Carr.

##### *Juniper*

*Transverse.* Growth rings variable, more or less eccentric and often coalescent. Summer wood thin, chiefly of 3–6 tracheids, not very dense, passing somewhat abruptly into the broad spring wood. Spring wood rather open, the tracheids squarish, the walls medium. Resin cells numerous and conspicuous, chiefly in broad, open bands. Medullary rays very prominent and resinous, 1 cell wide, distant 2–11, rarely 17, tracheids.

*Radial.* Ray cells very resinous, more or less contracted at the ends, equal to 5–7 spring tracheids; the upper and lower walls medium and entire or remotely pitted, becoming conspicuously thicker at the ends of the cells; the terminal walls thin, curved and entire or straight, locally thickened or even coarsely pitted; the lateral walls with oblong pits, chiefly 1, or in the marginal cells and low rays 2–4, per tracheid. Bordered pits broadly elliptical, rather numerous, the orifice rather large. Pits on the tangential walls of the summer tracheids numerous and prominent, rather large, the orifice bell-shaped. Resin cells about 12.5–20  $\mu$  wide, and many times longer, upwards of 215  $\mu$ .

*Tangential.* Rays low and rather broad, very resinous, the cells from narrowly oval in the lowest rays to round or more rarely transversely oval, chiefly round.

A small tree rarely 6–9 m. high, with a trunk .30–.60 m. in diameter.

Wood light, soft, very close grained and compact, very durable in contact with the soil.

Relative specific gravity . . . . .	0.6282
Percentage of ash residue . . . . .	0.73
(Sargent)	

Dry slopes and plains of the lower Sacramento River, southward through the California coast ranges to Lower California; spreading inland along the coast mountains to their union with the Sierra Nevada, through which it ranges northward as far as Kernville, descending to 2600 feet; desert slopes of Tehachapi Mountains, and abundant on the northern foothills and on the seaward slopes of the San Jacinto and Cuyamaca ranges (Sargent).

From the Quaternary deposits (Iowan?) of the Klamath River, Orleans, Humboldt County, California, in blue, sandy silt at a depth of 150 feet. Material very slightly silicified and in a good state of preservation.

5. *J. utahensis*, Lemm.*Juniper*

*Transverse.* Growth rings very variable, chiefly thin. Summer wood very thin, of 2-4 tracheids, the transition to the spring wood somewhat abrupt. Spring wood rather open, the tracheids uniform, squarish-hexagonal, often radially compressed, rather large, the walls medium. Resin cells numerous, conspicuous, in very open bands in both the spring and summer wood. Medullary rays very prominent and resinous, broad, 1 cell wide, distant 2-8, more rarely 12, tracheids.

*Radial.* Ray cells more conspicuously contracted at the ends and distinctly less resinous than in the preceding, the resin chiefly in terminal masses, equal to 6-10 spring tracheids; the upper and lower walls not conspicuously thickened at the ends of the cells, thickish, rather uniform, obscurely pitted, if at all; the terminal walls often curved and coarsely pitted; the lateral walls with oblong pits, often with an obscure border, chiefly 1-2, or in the lowest rays 4, per tracheid. Pits on the tangential walls of the summer tracheids very numerous and large, but less open and prominent than in *J. californica*. Resin cells about 15  $\mu$  wide, very long, — 150  $\mu$  or upwards of 285  $\mu$ , — not strongly resinous.

*Tangential.* Rays somewhat resinous, the cells thick-walled, chiefly transversely oval or oblong, usually broader than in No. 4 and much shortened vertically.

A small tree 6-9 m. high, with a trunk .60-.90 m. in diameter. Wood light, soft, close grained, compact, very durable in contact with the soil.

Relative specific gravity . . . . .	0.5522
Percentage of ash residue . . . . .	0.75
(Sargent)	

Western base of Wasatch Mountains, Utah, to eastern California and south through the Great Basin to southern California; the San Francisco Mountains of eastern Arizona (Sargent).

6. *J. sabinoides*, Neés.*Cedar. Rock Cedar*

*Transverse.* Growth rings very variable. Summer wood rather dense and composed of small tracheids, often double, chiefly much less than the spring wood, into which it passes gradually and which it sometimes equals. Spring wood chiefly somewhat open, but the demarcation from the summer wood obscure. Resin cells numerous, not very resinous or prominent, usually in somewhat compact zones, chiefly of the summer wood. Medullary rays not very prominent, 1 cell wide, distant 2-8, rarely 12, rows of tracheids.

*Radial.* Ray cells rather resinous, equal to 5-10 spring tracheids; the upper and lower walls rather thick, variable, frequently pitted; the terminal walls thin and not pitted except in the marginal cells;

the lateral walls with 1-4 pits per tracheid. Bordered pits numerous, in 1 row, round or vertically compressed in compact rows, the lenticular orifice large. Pits on the tangential walls of the summer tracheids numerous and prominent. Resin cells not very numerous, 15-20  $\mu$  wide and 150-275  $\mu$  long.

*Tangential.* Rays usually very low, the cells oval to oblong, not broad, chiefly oval, barely resinous.

A tree 11-15 m. in height, with a trunk upwards of .30 m. in diameter. Wood light, hard, not strong, very close grained, compact, very durable in contact with the soil.

Relative specific gravity . . . . .	0.6907
Percentage of ash residue . . . . .	0.47
Approximate relative fuel value . . . . .	68.75
Coefficient of elasticity in kilograms on millimeters . . . . .	734.
Ultimate transverse strength in kilograms . . . . .	200.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	8505.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	4464.
(Sargent)	

Valley of the Colorado River, western Texas (Sargent).

#### 7. *J. communis*, Linn.

*Juniper. Ground Cedar*

*Transverse.* Growth rings medium, very variable. The chiefly thin and dense summer wood often double, sometimes equal to the spring wood, into which it passes very gradually, the line of demarcation obscure. Tracheids of the usually broad spring wood small. Resin cells rather numerous, usually not very prominent, in 1-3 very narrow zones in each growth ring, the contiguous tracheids rarely becoming resinous so as to form a strongly resinous zone. Medullary rays numerous, 1 cell wide, distant 2-8, or more rarely 10, rows of tracheids.

*Radial.* Rays uniformly resinous throughout, tracheids occasionally present and marginal. Ray cells somewhat contracted at the ends, equal to 5-6 spring tracheids; the upper and lower walls thick, unequal, rather frequently pitted; the terminal walls thin, entire, locally thickened or sometimes coarsely pitted; the lateral walls with unequally bordered, oval pits having a large, lenticular orifice, 1-2 per tracheid. Pits on the tangential walls of the summer tracheids rather numerous, not very large or prominent. Resin cells 12.5-15  $\mu$  wide, 125-200  $\mu$  long. Bordered pits round, equal to the tracheid, in 1 row, rather distant, or when more crowded becoming elliptical.

*Tangential.* Rays numerous, low, narrow, resinous; the oblong cells thick-walled.

A prostrate shrub with ascending branches, forming dense mats upwards of 5-7 m. in diameter and 1-1.30 m. high.

From Labrador to the Pacific (Macoun); southward to New Jersey and Pennsylvania; westward to Michigan and western Nebraska, thence southward through the Rocky Mountains to New Mexico (Britton).

### 8. *J. sabina*, Linn.

#### *Shrubby Red Cedar*

*Transverse.* Growth rings unequal, often coalescent on the narrower side.

The thin summer wood of 3-8 tracheids, rarely forming the entire ring, in the broader rings becoming double or treble. Spring wood open, the tracheids large and thin-walled. Resin cells not very numerous or prominent, chiefly narrowly zonate in the spring wood, often showing extensive but local aggregations when they become large, rounded and loosely grouped in irregular masses with the partial formation of resin canals. Medullary rays inconspicuous, distant 2-25, rarely 37, tracheids.

*Radial.* Ray cells very sparingly resinous, chiefly straight, equal to about 5 spring tracheids; the upper and lower walls thin and entire or with rather distant pits; the terminal walls thin and locally thickened or coarsely pitted; the lateral walls with rather prominent pits with a broadly lenticular or oval orifice, the border rather obscure, 1-2, chiefly 4, per tracheid. Bordered pits numerous, as broad as the tracheids, generally elliptical in 1 compact row, the orifice large. Pits on the tangential walls of the summer tracheids somewhat numerous and prominent. Resin cells about 15  $\mu$  wide, 125-150  $\mu$  long.

*Tangential.* Rays all narrow, the cells chiefly narrowly oval to oblong, the walls thin, variable; when of a single cell, the latter is high, lenticular.

A depressed, usually procumbent shrub, seldom more than 1.20 m. high (Britton).

On exposed slopes and river banks from Anticosti, Nova Scotia, New Brunswick, Quebec, and Ontario, across the prairie region to the summit of the Rocky Mountains at Kicking Horse Pass (Macoun); from Maine, westward through New York, Minnesota, and Montana (Britton).

### 9. *J. pachyphlæa*, Torr.

#### *Juniper. Checkered-Barked Juniper*

*Transverse.* Growth rings very narrow and unequal, eccentric. Summer wood dense and thin, of 2-6 tracheids, the transition to the spring wood somewhat gradual. Spring wood somewhat open, the tracheids in regular rows. Resin cells numerous, chiefly in the spring wood, irregularly zonate. Medullary rays very prominent and resinous, 1 cell wide, broad, distant 2-8 tracheids.

*Radial.* The resinous ray cells equal to 4-13 spring tracheids; the upper and lower walls medium to thick, entire or remotely pitted; the terminal walls strongly pitted; the lateral walls with rather conspicuous, lenticular pits about 1-2, more rarely 4, per tracheid. Bordered pits



round, numerous, becoming very small and obscure in the summer wood, the round orifice becoming lenticular towards the summer wood. Pits on the tangential walls of the summer tracheids numerous, medium, flat. Resin cells about 20  $\mu$  wide, 165–400  $\mu$  long.

*Tangential.* Rays medium, often 2-seriate in part, the cells broadly oval or round, rather thick-walled.

A tree 6–15 m. high and .60 m. in diameter.

Wood light, soft, not strong, brittle, very close grained, compact, susceptible of a fine polish.

Relative specific gravity . . . . .	0.5829
Percentage of ash residue . . . . .	0.11
(Sargent)	

Mountains of western Texas, southern New Mexico, and Arizona south of latitude 34°; southward into Mexico (Sargent).

#### 10. *J. monosperma*, Sarg.

##### *Juniper*

*Transverse.* Growth rings chiefly broad, very variable. The prominent but usually very thin summer wood dense, of 3–7 tracheids, often double; the transition from the spring wood somewhat gradual. Spring wood somewhat dense, the tracheids variable. Resin cells very prominent and resinous, numerous, in compact zones chiefly in the spring wood. Medullary rays very numerous and prominent, broad, 1 cell wide, distant 1–10 rows of tracheids.

*Radial.* Ray cells resinous throughout, more or less conspicuously contracted at the ends, equal to 6–8 spring tracheids; the upper and lower walls thick, rather uniform, frequently pitted; the terminal walls coarsely pitted; the lateral walls with small, round, bordered pits with a lenticular-oblong but small orifice, chiefly 2, but in low rays and marginal cells often upwards of 6, per tracheid. Bordered pits numerous and in 1 compact row, round or vertically compressed, nearly as broad as the tracheid. Pits on the tangential walls of the summer tracheids very numerous but small. Resin cells about 15  $\mu$  wide, 200  $\mu$  and upwards long.

*Tangential.* Rays numerous, resinous, low; the broad cells oval or round, somewhat uniform.

A stunted tree 6–9 m. high, and a trunk upwards of .60 m. in diameter.

Relative specific gravity . . . . .	0.7119
Percentage of ash residue . . . . .	0.78
(Sargent)	

Gravelly slopes between 3500 and 7000 feet elevation, eastern base of Pikes Peak, to the mountains of western Texas; through New Mexico and southern Arizona to southern California (Sargent).

11. *J. occidentalis*, Hook.*Juniper*

*Transverse.* Growth rings usually very narrow; the dense summer wood of 2-4, rarely 10, tracheids, passing rather abruptly into the rather open spring wood; the tracheids small and thick-walled. Spring wood rather open, but the tracheids rather small and usually much rounded. Resin cells abundant and prominent, chiefly in the summer and outer spring wood, in open or compact zones. Medullary rays numerous, rather prominent, not very resinous, 1 cell wide, distant 2-8, rarely 13, rows of tracheids.

*Radial.* Ray cells very sparingly resinous, usually straight or somewhat contracted at the ends, equal to 4-6 spring tracheids; the upper and lower walls thickish, entire or distantly pitted; the terminal walls strongly pitted; the lateral walls with small, oval, bordered pits, the orifice oblong, 1-3, more rarely 4, per tracheid throughout. Bordered pits round, numerous, in 1 row, becoming obscure or wanting in the summer wood. Pits on the tangential walls of the summer tracheids numerous, but usually small and often obscure. Resin cells numerous, 20  $\mu$  wide, 140-275  $\mu$  long.

*Tangential.* Rays generally low, of a few cells only; the cells round to oblong, not very broad, chiefly oval.

A tree 6-15 m. high, with a trunk 1.20-2.10 m. in diameter; often becoming a low, much-branched shrub.

Wood light, soft, very close grained, compact, very durable in contact with the soil.

Relative specific gravity . . . . .	0.5765
Percentage of ash residue . . . . .	0.12
(Sargent)	

Dry, rocky ridges and prairies of the Blue Mountains and high prairies of eastern Washington and Oregon; the Cascade Mountains of Oregon; the valley of the Klamath River, California, and south along the high ridges of the Sierra Nevada Mountains at elevations of 7000-10,000 feet, to the San Bernardino Mountains (Sargent).

12. \* *ABIES*, LINK. PLATES 42 AND 43

*Transverse.* Growth rings usually broad with no very clear demarcation between the spring and summer woods. Resin passages sometimes present and then imperfectly organized, usually in somewhat distant growth rings. Resin cells, when present, remote and inconspicuous on the outer face of the summer wood.

*Radial.* Ray tracheids not present (except *A. balsamea*). The terminal walls of the ray cells usually strongly pitted, especially in the summer wood. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting. Rays narrow, strictly 1-seriate.

## SYNOPSIS OF SPECIES

1. Resin passages present but imperfectly developed<sup>1</sup>

Ray cells (tangential) all broad, oval, or round.

Pits on the lateral walls of the ray cells 1-3, rarely 4, per tracheid.

Tracheids in regular rows.

Resin cells on the outer face of the summer wood.

10. *A. concolor*.

Resin cells wanting.

8. *A. bracteata*.

Pits on the lateral walls of the ray cells chiefly 2, rarely 3-4, per tracheid.

Tracheids in regular rows.

Resin cells wanting.

9. *A. nobilis*.

Ray cells uniformly narrow, oblong.

Pits on the lateral walls of the ray cells obscurely bordered, greatly reduced or wanting in the summer wood, 1-4, or in the marginal cells 6, per tracheid.

Resin cells wanting.

11. *A. firma*.

## 2. Resin passages wholly wanting

Ray tracheids present, few.

Resin cells (transverse) wanting.

Ray cells (tangential) uniformly narrow, oblong.

Pits on the lateral walls of the ray cells 1-4, rarely 8, per tracheid.

4. \* *A. balsamea*.

Ray tracheids wholly wanting.

Resin cells wanting.

Ray cells (tangential) uniformly narrow.

Pits on the lateral walls of the ray cells 1-4, rarely 8, per tracheid.

4. \* *A. balsamea*.

Pits on the lateral walls of the ray cells obscurely bordered, greatly reduced or wanting in the summer wood, 1-4, or in the marginal cells 6, per tracheid.

11. *A. firma*.

Pits on the lateral walls of the ray cells more or less obviously bordered, especially in the summer wood, chiefly 2 per tracheid.

1. *A. Fraseri*.

Ray cells (tangential) variable, from round or oval to narrowly oblong.

<sup>1</sup> Species included in this section should also be looked for under the second section with the same differentiation.

Pits on the lateral walls of the ray cells 1-4, in the marginal cells rarely 5, per tracheid.

Upper and lower walls of the ray cells strongly pitted throughout.

2. *A. lasiocarpa*.

Pits on the lateral walls of the ray cells 1-2, or in the marginal cells upwards of 4, per tracheid.

Upper and lower walls of the ray cells sparingly pitted in the spring wood.

3. *A. Veitchii*.

Resin cells scattering on the outer face of the summer wood.

Ray cells broad (tangential), oval to round.

Pits on the lateral walls of the ray cells small, round, or oval, at first obscurely bordered, but toward the summer wood with a distinct border and narrow orifice.

Pits on the lateral walls of the ray cells 1-4, soon becoming 2, and in the summer wood 1, per tracheid throughout.

Upper and lower walls of the ray cells thin, not obviously pitted.

Ray cells (tangential) very broad and large.

7. *A. grandis*.

Pits on the lateral walls of the ray cells 1-2, rarely 3, or in the marginal cells sometimes 5, per tracheid.

Upper and lower walls of the ray cells thick, unequal, coarsely but very unequally pitted.

Ray cells (tangential) chiefly oval, rarely in pairs.

6. *A. amabilis*.

Pits on the lateral walls of the ray cells chiefly 2, more rarely 1 or 4, or in the summer wood 1, per tracheid throughout.

Upper and lower walls of the ray cells unequal, strongly but imperfectly pitted throughout.

Ray cells (tangential) round or oval, not very large.

5. *A. magnifica*.

1. *A. Fraseri*, Poir.

*Balsam. She Balsam*

*Transverse.* Growth rings rather thin, variable, the structure open throughout. Summer wood very thin, of 2-6 tracheids, passing gradually into the spring wood. Spring tracheids rather large and thin-walled,

squarish, uniform, in very regular rows. Resin cells none. Resin-bearing tracheids few, rather prominent, scattering through the summer wood, more rarely in the spring wood. Medullary rays somewhat resinous and prominent, 1 cell wide, distant 2-15 rows of tracheids.

*Radial.* Medullary rays sparingly resinous throughout, wholly devoid of tracheids. Ray cells straight, or in the summer wood contracted at the ends, equal to 7-8 spring tracheids; the upper and lower walls medium, unequal, somewhat distantly and imperfectly pitted in the spring wood, but strongly pitted in the summer wood; the terminal walls strongly pitted; the lateral walls with small pits which become conspicuously bordered in the summer wood where the orifice is reduced to a slit and the pit is round, 1-2, chiefly 2, or in the marginal cells 2-4, per tracheid. Resin-bearing tracheids not numerous, the resin sometimes massive in the summer wood, but forming a peripheral layer in the spring wood. Bordered pits elliptical, in 1 row or sometimes in pairs. Pits on the tangential walls of the summer tracheids somewhat numerous but small and flat.

*Tangential.* Rays small to medium, the cells narrow, rather uniform, oval to oblong.

A tree 18-24 m. high and upwards of .60 m. in diameter.

Wood very light, soft, not strong, coarse grained, compact.

Relative specific gravity . . . . .	0.3565
Percentage of ash residue . . . . .	0.54
Approximate relative fuel value . . . . .	35.46
Coefficient of elasticity in kilograms on millimeters . . . . .	972.
Ultimate transverse strength in kilograms . . . . .	273.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5557.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1048.
(Sargent)	

High mountains of North Carolina and Tennessee, forming somewhat extensive forests on moist slopes between 5000 and 6500 feet (Sargent).

## 2. *A. lasiocarpa*, Nutt.

### *Mountain Balsam. Balsam Fir*

*Transverse.* Growth rings narrow, uniform, the structure open throughout. Summer wood very thin, rarely upwards of 14 tracheids, the transition to the spring wood gradual. Spring wood of large, squarish tracheids with rather thin walls, uniform in regular rows. Resin cells and resinous tracheids wholly wanting. Medullary rays not prominent, barely if at all resinous, 1 cell wide, distant 2-8, more rarely 15, tracheids.

*Radial.* Rays very sparingly resinous, wholly devoid of tracheids. Ray cells more or less conspicuously contracted at the ends, equal to about 7 spring tracheids; the upper and lower walls thick, unequal, and strongly pitted throughout; the terminal walls thin, often devoid of pits; the lateral walls with obscurely bordered pits, the large orifice lenticular, variable, 1-4, or in the marginal cells rarely 5, per tracheid, and distinctly bordered, in the summer wood reduced to 1 per tracheid

and distinctly bordered. Bordered pits elliptical, in 1 row, nearly the diameter of the tracheid. Pits on the tangential walls of the summer tracheids rather numerous, not very large. Resin cells and resinous tracheids wholly wanting.

*Tangential.* Rays medium, the cells variable, from round or broadly oval to narrowly oblong.

A tree 20-40 m. high, with a trunk upwards of .60 m. in diameter.

Wood very light, soft, not strong, rather close grained, compact.

Relative specific gravity . . . . .	0.3476
Percentage of ash residue . . . . .	0.44
Approximate relative fuel value . . . . .	34.61
Coefficient of elasticity in kilograms on millimeters . . . . .	762.
Ultimate transverse strength in kilograms . . . . .	202.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4829.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1015.
(Sargent)	

Summit of House Mountain, south of Lesser Slave Lake; abundant in Bow River Pass on mountain slopes 5000-7000 feet elevation, extending on the line of the Central Pacific Railroad from Castle Mountain to Selkirk Summit; abundantly in the Gold and Selkirk ranges, and in the Rocky Mountain region east of McLeod's Lake; elsewhere in the northern portion of the interior plateau it occurs in scattering groves, generally in localities nearly reaching or surpassing 4000 feet, but even in low valleys in the eastern portion of the coast ranges; damp situations in the country between Lesser Slave Lake and the Athabasca River; high, cool valleys in the Rocky Mountains, southward to the 49th parallel, reaching upward to the timber line (Macoun); valley of the Stakhin River in Alaska, in latitude 60° N.; through the Blue Mountains of Oregon and the ranges of Idaho, Montana, Wyoming, Utah, and Colorado; on mountain slopes and cañons from 4000 (British Columbia) to 12,000 feet (Colorado); rarely forming the prevailing forest growth (Sargent).

### 3. *A. Veitchii*, Lindl.

*Jap.* = *Shirabé*

*Transverse.* Growth rings very variable, often very narrow. Summer wood prominent but very narrow, of 3-5 squarish tracheids, the structure open, or again broad and somewhat exceeding the spring wood, with the structure rather open but the tracheids strongly rounded; transition to the spring wood gradual. Spring wood open, the tracheids rather large, squarish, and thin-walled, uniform in regular rows. Resin cells and resinous tracheids wanting. Medullary rays not prominent, 1 cell wide, distant 1-20 rows of tracheids.

*Radial.* Rays somewhat resinous in part, and wholly devoid of tracheids. Ray cells chiefly straight, equal to 7-8 spring tracheids, or in the

summer wood becoming very much shorter; the upper and lower walls medium, unequal, the narrow pits not very numerous, except in the summer wood, often imperfectly formed; the terminal walls closely pitted, becoming more prominent in the summer wood; the lateral walls with narrowly bordered oval pits, 1-2, or in the marginal cells upwards of 4, per tracheid, the orifice broadly lenticular or oval. Bordered pits round or elliptical, numerous in 1 row, variable, but chiefly two thirds the diameter of the tracheid, the large orifice round. Pits on the tangential walls of the summer tracheids few, small, rather open. Resin cells and resinous tracheids wholly wanting.

*Tangential.* Rays not very numerous, medium to high, somewhat resinous, strictly 1-seriate; the cells somewhat unequal and variable, chiefly round or oval, sometimes oblong.

#### 4. \* *A. balsamea*, Mill.

*Balsam Fir. Balm-of-Gilead Fir. Canada Balsam Fir*

*Transverse.* Growth rings thick. Summer wood thin, open, passing very gradually into the spring wood. Spring wood very open, the large tracheids squarish-hexagonal, thin-walled, uniform in regular rows. Resin cells wanting. Medullary rays not numerous or prominent, 1 cell wide, distant 2-8, rarely 12, rows of tracheids.

*Radial.* Ray tracheids few, narrow, and very unequal; the rays barely resinous. Ray cells conspicuously contracted at the ends and equal to 2-6 spring tracheids; the upper and lower walls medium, unequal, somewhat distantly and finely, but often imperfectly, pitted; the terminal walls coarsely pitted, especially in the summer wood; the lateral walls with small, round or oval pits, 2-4, more rarely upwards of 8, per tracheid. Bordered pits elliptical, large, one half the diameter of the tracheid, chiefly rather scattering, in 1 row or often in pairs, and more or less imperfectly 2-rowed. Pits on the tangential walls of the summer wood not numerous, chiefly quite small.

*Tangential.* Rays medium, the cells narrow, uniform, oval to oblong.

A tree 21-27 m. high, with a trunk upwards of .60 m. in diameter.

Wood very light, soft, not strong, coarse grained, compact, not durable.

Relative specific gravity . . . . .	0.3819
Percentage of ash residue . . . . .	0.45
Approximate relative fuel value . . . . .	38.02
Coefficient of elasticity in kilograms on millimeters . . . . .	819.
Ultimate transverse strength in kilograms . . . . .	220.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5851.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1202.
(Sargent)	

Abundant in swamps throughout the eastern provinces of Canada, northward to James Bay and westward to the Athabasca River in latitude 58° (Macoun); southward through the northern United States to Pennsylvania, and along the Allegheny Mountains to the high peaks of Virginia;

westward through central Michigan and Minnesota and northward along the eastern slope of the Rocky Mountains (Sargent).

Pleistocene of the Scarborough Period at Scarborough, Ontario.

Material altered by decay, but otherwise in original condition and not petrified.

### 5. *A. magnifica*, A. Murr.

#### *Red Fir*

*Transverse.* Growth rings rather broad. The summer wood upwards of one third the growth ring, the structure open throughout, but the most recent tracheids much compressed radially, transition to the spring wood very gradual. Spring wood open, the large, conspicuously squarish tracheids uniform in very regular rows, thin-walled. Resin cells present on the outer face of the summer wood, where they are to be distinguished by their thin walls and somewhat advanced position. Medullary rays prominent, sparingly resinous, 1 cell wide, distant 2–10 rows of tracheids.

*Radial.* Rays sparingly resinous throughout and wholly devoid of tracheids. Ray cells straight throughout, equal to 7–9 spring tracheids, becoming much shorter in the summer wood; the upper and lower walls thick, unequal, and strongly but imperfectly pitted throughout; the terminal walls sparingly pitted in the spring wood, but becoming strongly pitted in the summer wood; the lateral walls with small, obscurely bordered pits, at length becoming conspicuous and round with a prominent border and slitlike orifice toward the summer wood, chiefly 2, more rarely 1 or 4, in the summer wood reduced to 1, per tracheid throughout. Bordered pits in 1 row, elliptical, becoming much smaller toward the summer wood, where the round orifice becomes narrow and prolonged, coalescing to form spiral striations. Pits on the tangential walls of the summer tracheids numerous but flat and small, sometimes present on the tangential walls of the earliest spring tracheids. Resin cells few, on the outer face of the summer wood, nonresinous and distinguished by the transverse septa without bordered pits; narrow and very long, usually about 20–25  $\mu$  wide, 350–435  $\mu$  or more long.

*Tangential.* Rays high, occasionally 2-seriate in part, the cells uniformly broad, round, and large or oval, sometimes sparingly resinous.

A large tree 61–76 m. high, with a trunk 2.40–3 m. in diameter.

Wood light, soft, not strong, rather close grained, compact, satiny, durable in contact with the soil, liable to twist and warp in seasoning.

Relative specific gravity . . . . .	0.4701
Percentage of ash residue . . . . .	0.30
Approximate relative fuel value . . . . .	46.87
Coefficient of elasticity in kilograms on millimeters . . . . .	662.
Ultimate transverse strength in kilograms . . . . .	299.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6963.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1545.

(Sargent)



California, Mt. Shasta, south along the western slopes of the Sierra Nevadas to Kern County; forming extensive forests between 4900 and 8000 feet elevation; becoming less common south of Mt. Shasta, and reaching an extreme elevation of 10,000 feet (Sargent).

### 6. *A. amabilis*, Forbes

#### *White Fir*

*Transverse.* Growth rings narrow, the structure usually very open throughout. Summer wood upwards of one half the spring wood, into which it passes very gradually. Spring tracheids large, thin-walled, very squarish, and uniform in regular rows. Resin cells few and widely scattering on the outer face of the summer wood, where they may be distinguished by (1) the sieve-plate structure of the terminal wall, and (2) their often advanced position. Medullary rays rather prominent, not resinous, 1 cell wide, numerous, distant 2-9 rows of tracheids.

*Radial.* Rays nonresinous, wholly devoid of tracheids. Ray cells chiefly straight except in the summer wood, equal to 3-7 spring tracheids, becoming much shorter in the summer wood; the upper and lower walls thick, unequal, and coarsely but very unequally pitted throughout; the terminal walls strongly pitted throughout; the lateral walls with small, round or oval pits, which toward the summer wood show a prominent and broad border, and the broadly lenticular orifice becomes reduced to a slit, 1-2, rarely 3, or in the marginal cells sometimes 5, per tracheid. Bordered pits in 1 row, sometimes in pairs, variable, elliptical. Pits on the tangential walls of the summer tracheids numerous and rather small, but broadly lenticular, open. Resin cells frequently present on the outer face of the summer wood, sometimes conterminous with similar tracheids; usually very narrow and long, 12.5-25  $\mu$  wide, and upwards of 600  $\mu$  long.

*Tangential.* Rays medium to high, the cells uniform, chiefly oval, more rarely round or narrowly oval, sometimes in pairs.

A tree 30-45 m. high, with a trunk upwards of 1.20 m. in diameter.

Wood light, hard, not strong, close grained, compact.

Relative specific gravity . . . . .	0.4228
Percentage of ash residue . . . . .	0.23
Approximate relative fuel value . . . . .	42.18
Coefficient of elasticity in kilograms on millimeters . .	1260.
Ultimate transverse strength in kilograms . . . . .	338.
Ultimate resistance to longitudinal crushing in kilograms	7480.
Resistance to indentation to 1.27 mm. in kilograms . .	1029.

(Sargent)

Valley of the Fraser River and probably farther north; south along the Cascade Mountains of Washington and Oregon (Sargent).

7. *A. grandis*, Lindl.*White Fir*

*Transverse.* Growth rings usually very broad, the structure rather open throughout. Summer wood prominent, upwards of one eighth to one fourth the very broad spring wood, into which it passes gradually, the tracheids very unequal. Spring tracheids very large, thin-walled, hexagonal, in regular rows, rather uniform. Resin cells few and scattering on the outer face of the summer wood, nonresinous, distinguished by (1) the sieve-plate structure of the terminal walls, and (2) their somewhat advanced position. Resin-bearing tracheids more or less numerous and scattering through the summer wood. Resin passages wholly wanting. Medullary rays rather prominent and resinous, especially in the summer wood, 1 cell wide, distant 2-8, or rarely 10-12, rows of tracheids.

*Radial.* Rays more or less resinous throughout. Ray cells straight, becoming contracted at the ends in the summer wood, equal to 4-6 spring tracheids; the upper and lower walls thin and entire or sparingly and imperfectly pitted; the terminal walls at first barely if at all pitted, but at length coarsely pitted in the summer wood; the lateral walls with prominent but small oval pits, with an obscure border, the latter becoming prominent toward the summer wood, where the broadly lenticular orifice becomes oblong, 1-2 throughout, or more rarely 4-6 in the marginal cells. Bordered pits rather numerous in 1 row, elliptical but variable, the orifice large. Resin-bearing tracheids rather numerous and chiefly in contact with the rays, very resinous. Resin cells on the outer face of the summer wood rather prominent, long, and narrow, nonresinous, about equal to  $20\ \mu$  wide and  $135-310\ \mu$  long. Pits on the tangential walls of the summer tracheids somewhat numerous, rather small and flat.

*Tangential.* Rays rather numerous, low to high, broad, the rather large cells more or less unequal, chiefly broadly oval, often squarish, frequently resinous.

A tree 61-92 m. high, with a trunk .90-1.50 m. in diameter.

Wood light, soft, not strong, coarse grained, compact.

Relative specific gravity . . . . .	0.3545
Percentage of ash residue . . . . .	0.49
Approximate relative fuel value . . . . .	35.08
Coefficient of elasticity in kilograms on millimeters . . . . .	958.
Ultimate transverse strength in kilograms . . . . .	211.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6255.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	810.
(Sargent)	

Vancouver Island, south to Mendocino County, California, near the coast; interior valleys of western Washington and Oregon, south to the Umpqua River, Cascade Mountains below 4000 feet elevation; Blue Mountains of Oregon; Bitter Root Mountains of Idaho; western slopes of the Rocky Mountains of northern Montana (Sargent).

8. *A. bracteata*, Nutt.*Silver Fir*

*Transverse.* Growth rings broad. Summer wood prominent, dense, one third the spring wood, into which it passes somewhat gradually. Spring wood rather open, the tracheids large and thin-walled, squarish-hexagonal, rather uniform in regular rows. Resinous tracheids wholly wanting. Resin cells sometimes present and then forming imperfectly organized resin canals in a somewhat continuous zone, within or near the summer wood of distant growth rings. Medullary rays prominent and somewhat resinous, especially in the summer wood, 1 cell wide.

*Radial.* Rays somewhat resinous throughout, especially in the summer wood, wholly devoid of tracheids. Ray cells straight or barely fusiform except in the summer wood, where they are strongly contracted at the ends; equal to about 5 spring tracheids; the upper and lower walls rather thin, unequal, rather distantly pitted except in the summer wood, where the pits are numerous, or again in the spring wood locally numerous; the terminal walls thin, often devoid of pits except in the summer wood; the lateral walls with prominent, round or broadly oval pits, chiefly 1-3, or in the marginal cells 4, per tracheid. Bordered pits numerous, chiefly elliptical in 1 row, or often in pairs so that they become more or less 2-rowed. Pits on the tangential walls of the summer wood numerous and extending well into the interior. Resin cells short-cylindrical, united to form short resin sacs on the outer face of the summer wood.

*Tangential.* Rays medium to high; the cells chiefly broad, oval, often resinous and sometimes in pairs of much smaller cells.

A tree 41-61 m. in height and with a trunk .90-1.20 m. in diameter.

Wood heavy, not hard, coarse grained, compact.

Relative specific gravity . . . . .	0.6783
Percentage of ash residue . . . . .	2.04
(Sargent)	

Santa Lucia Mountains of California, from the northern boundary of San Luis Obispo County, about 40 miles northward; on moist, cold soil, occupying four or five cañons at 3000-6000 feet elevation, generally west of the summit of the range (Sargent).

9. *A. nobilis*, Lindl.*Red Fir. Larch*

*Transverse.* Growth rings rather broad. The summer wood prominent, broad, upwards of one half the spring wood, the structure chiefly open, but becoming rather dense on the outer face of the growth ring; transition to the spring wood gradual. Spring tracheids rather large and thin-walled, squarish-hexagonal, toward the summer wood becoming unequal and in more or less irregular rows. Resin cells localized

to form imperfect resin canals in a more or less continuous zone in the summer wood of distant growth rings. Medullary rays prominent, somewhat resinous, 1 cell wide, distant 1-8 rows of tracheids.

*Radial.* Rays more or less resinous throughout, wholly devoid of tracheids. Ray cells chiefly straight, becoming conspicuously fusiform in the summer wood, equal to about 8-11 spring tracheids; the upper and lower walls medium, unequal, more or less strongly pitted throughout; the terminal walls strongly pitted; the lateral walls with round or oval, conspicuously bordered pits, the orifice lenticular or oblong, 1-2, or in the marginal cells rarely 3-4, per tracheid. Bordered pits in 1 row, sometimes in pairs, round, the orifice large. Pits on the tangential walls of the summer tracheids minute. Resin cells, when present, short-cylindrical and united to form short resin sacs within the summer wood of distant growth rings.

*Tangential.* Rays medium to high, the cells often resinous, chiefly broad but variable from round to oval and oblong, unequal, often in pairs.

A large tree 61-92 m. high, with a trunk 2.40-3 m. in diameter.

Wood light, hard, strong, rather close grained, compact.

Relative specific gravity . . . . .	0.4561
Percentage of ash residue . . . . .	0.34
Approximate relative fuel value . . . . .	45.46
Coefficient of elasticity in kilograms on millimeters . . . . .	1277.
Ultimate transverse strength in kilograms . . . . .	368.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7256.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1917.
(Sargent)	

Oregon, Cascade Mountains from the Columbia River south to the valley of the upper Rogue River, and along the summits of the Coast Range from the Columbia to the Nestucca River (Sargent).

#### 10. *A. concolor*, Lindl. and Gordon

##### *White Fir. Balsam Fir*

*Transverse.* Growth rings broad, the structure rather open throughout.

Summer wood prominent, thin, upwards of one third the spring wood, into which it passes very gradually. Spring tracheids medium, squarish, thin-walled, and uniform in somewhat regular rows. Resin passages prominent and rather numerous but imperfectly formed, very variable, and often large, forming more or less continuous series within the summer wood, often of distant growth rings. Resin cells few, nonresinous, distant on the outer face of the summer wood and distinguished by (1) the sieve-plate structure of the terminal wall, and (2) their somewhat advanced position. Medullary rays rather prominent and somewhat resinous, especially in the summer wood; 1 cell wide, distant 2-7, rarely 10, rows of tracheids.

*Radial.* Rays somewhat resinous, especially in the summer wood. Ray cells conspicuously contracted at the ends throughout and equal to

6-11 spring tracheids, becoming shorter in the summer wood; the upper and lower walls rather thick, unequal, and conspicuously pitted throughout; the terminal walls rather sparingly pitted, especially in the spring wood; the lateral walls with round or elliptical, small, obscurely bordered pits, which become distinctly bordered toward the summer wood, where the broadly lenticular orifice becomes oblong or finally slitlike, 1-3 per tracheid throughout the spring wood, becoming 1 in the summer wood. Bordered pits rather numerous in 1 row, elliptical or round. Pits on the tangential walls of the summer tracheids rather numerous but not very large, flat. Pits rarely on the tangential walls of the earlier spring tracheids. Resin cells rarely to be seen. Resin passages imperfectly formed of short, cylindrical resin cells, in interrupted series.

*Tangential.* Rays numerous, medium to high, not very broad; the cells chiefly uniform, oval, sometimes round or oblong, rarely large.

A tree 30-40 m. in height, with a trunk 1.20-1.50 m. in diameter.

Wood very light, soft, not strong, coarse grained, compact.

Relative specific gravity . . . . .	0.3638
Percentage of ash residue . . . . .	0.85
Approximate relative fuel value . . . . .	36.07
Coefficient of elasticity in kilograms on millimeters . . . . .	909.
Ultimate transverse strength in kilograms . . . . .	300.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6237.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1248.
(Sargent)	

Moist slopes and cañons between 3000 and 9000 feet elevation, reaching its greatest development in the California Sierras; northern slopes of the Siskiyou Mountains of Oregon; south along the western slope of the Sierra Nevadas to San Bernardino and San Jacinto Mountains of California; the high mountains of Arizona to the Mogollon Mountains of New Mexico; northward to Pikes Peak and the Wasatch Mountains of Utah (Sargent).

# 11. *A. firma*, Sieb. et Zucc.

*Jap. = Momi*

*Transverse.* Growth rings broad, the dense summer wood about one fourth the spring wood, into which it passes gradually. Spring wood open, the tracheids thin-walled, in very regular rows, uniform, large. Resin cells and resinous tracheids wanting. Medullary rays rather prominent and sparingly resinous, 1 cell wide, distant 2-10 rows of tracheids. Resin canals present but imperfectly organized, forming local or sometimes extensive tangential rows on the outer face of the summer wood of distant growth rings.

*Radial.* Medullary rays sparingly resinous, devoid of tracheids. Ray cells straight, equal to 5-10 spring tracheids, in the summer wood becoming much shorter and distinctly fusiform; the upper and lower

walls medium, unequal, very sparingly pitted, in the summer wood becoming conspicuously thicker and strongly pitted; the terminal walls coarsely pitted, when seen in plan like a sieve plate; the lateral walls with obscurely bordered pits, 1-4, or in the marginal cells and low rays upwards of 6, per tracheid, becoming reduced toward the summer wood, where they are only 1 or entirely wanting. Bordered pits numerous, elliptical, usually less than half the tracheid, in 1 row or often in pairs and imperfectly 2-rowed. Pits on the tangential walls of the summer tracheids not very numerous, rather small. Resin cells and resinous tracheids wanting.

*Tangential.* Rays medium to high, sparingly resinous, narrow, strictly 1-seriate; the cells uniform, oblong, rarely oval.

### 13. TSUGA, CARR. PLATES 44 AND 45

*Transverse.* Growth rings usually thin, the summer wood prominent, usually dense. Resin passages rarely present (*T. heterophylla*) and then imperfectly organized. Resin cells scattering on the outer face of the summer wood and distinguished by (1) their resinous contents, (2) their somewhat advanced position, (3) their thinner walls, and (4) the sieve-plate structure of the terminal walls; rarely numerous and zonate in the spring or summer wood. Resinous tracheids wanting (except in *T. Mertensiana*).

*Radial.* Ray tracheids usually prominent, sometimes interspersed, usually marginal. Ray cells usually resinous, more or less contracted at the ends, the terminal walls strongly pitted. Tracheids wholly without spirals.

*Tangential.* Fusiform rays wholly wanting. Ray cells rarely in pairs, not broad, chiefly oval or round.

### SYNOPSIS OF SPECIES

Bordered pits in 2 rows.

Resin passages wholly wanting, the prominent resin cells scattering on the outer face of the summer wood.

Pits on the lateral walls of the ray cells 2-4, or in the summer wood 1-2, per tracheid.

1. *T. canadensis*.

Bordered pits in 1 row.

Resin passages present but imperfectly formed, in more or less continuous series, the resin cells scattering on the outer face of the summer wood.

Pits on the lateral walls of the ray cells 1-2, rarely 3, per tracheid.

Spring tracheids very large and uniform, distinctly 4-sided, the walls thin.

5. *T. Mertensiana*.

Resin passages not present.

Resin cells scattering on the outer face of the summer wood.

Pits on the lateral walls of the ray cells 2-4, or in the summer wood 1-2, per tracheid; the resin cells prominent, resinous.

1. *T. canadensis*.

Pits on the lateral walls of the ray cells 1-2, rarely 3, per tracheid.

Spring tracheids very large and uniform, conspicuously 4-sided, the walls thin.

5. *T. Mertensiana*.

Pits on the lateral walls of the ray cells very variable, at first 5, soon uniformly 2, and finally 1, per tracheid.

Spring tracheids squarish-hexagonal.

2. *T. Sieboldii*.

Resin cells on the outer face of the summer wood and also often zonate in the spring or summer wood.

Resinous tracheids wanting.

Pits on the lateral walls of the ray cells 2-6, finally 1, per tracheid.

3. *T. caroliniana*.

Resinous tracheids in groups or radial series in contact with the rays.

Pits on the lateral walls of the ray cells 1-4, chiefly 2, and finally 1, per tracheid, the orifice finally becoming a prolonged slit.

4. *T. Pattoniana*.

1. *T. canadensis*, Carr.

#### *Hemlock*

*Transverse.* Growth rings thin, variable. The thin and dense summer wood prominent, equal to about one fourth to one half the spring wood, from which the transition is abrupt. Spring wood very open, the large and very thin-walled tracheids conspicuously squarish, often elongated radially, very uniform and in regular rows. Resin cells prominent, resinous, not very numerous. Medullary rays very prominent, somewhat resinous, 1 cell wide, distant 2-10 rows of tracheids.

*Radial.* Rays uniformly somewhat resinous throughout, the tracheids often interspersed. Ray cells somewhat contracted at the ends, equal to 3-5 spring tracheids; the upper and lower walls medium, unequal, very irregularly and often imperfectly, sometimes very sparingly, pitted; the terminal walls not very strongly pitted except in the summer wood; the lateral walls with small, oval pits, at first with a very narrow border, which becomes more pronounced toward the

summer wood, the lenticular orifice becoming oblong, 2-4, or in the summer wood 1-2, per tracheid. Bordered pits round or elliptical in 1-2 rows, more rarely in 1 row only, the orifice large. Pits on the tangential walls of the summer wood rather numerous, prominent, flat. Resin cells 15  $\mu$  wide, 165-240  $\mu$  long.

*Tangential.* Rays numerous, low to high, not very broad, usually constricted at the position of the frequent narrow and oblong tracheids; the parenchyma cells rather equal and chiefly narrowly oval to oblong, sometimes broadly oval.

A tree 21-33 m. high and with a trunk .90-1.15 m. in diameter.

Wood light, soft, not strong, brittle, coarse, crooked grained, difficult to work, liable to wind shake and splinter, not durable (Sargent).

This wood is of great value for construction purposes, where it is to be constantly submerged in water, when it possesses elements of great durability (Bovey).

Relative specific gravity . . . . .	0.4239
Percentage of ash residue . . . . .	0.46
Approximate relative fuel value . . . . .	42.20
Coefficient of elasticity in kilograms on millimeters . . . . .	900.
Ultimate transverse strength in kilograms . . . . .	307.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6142.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1314.

(Sargent)

According to the results obtained by Dr. Bovey in the testing laboratories of McGill University, the following data may be given:

Coefficient of strength in pounds per square inch for:

Bending . . . . .	5000
Torsion . . . . .	8000
Compression . . . . .	3200
Shear . . . . .	380
Weight of 1 cubic foot . . . . .	33

Abundant on cold soils, Nova Scotia and New Brunswick, and throughout Quebec and Ontario; northward from Quebec to the northern end of Lake Temiscaming, thence to the eastern extremity of Lake Superior at Agawa (Macoun); through the northern United States to Newcastle County, Delaware, and along the Allegheny Mountains to Clear Creek Falls, Winston County, Alabama; southeastern Michigan and central Wisconsin (Sargent).

## 2. *T. Sieboldii*, Carr.

*Jap.* = *Tsuga*

*Transverse.* Growth rings narrow, uniform, the prominent summer wood dense, about one fourth to one half the spring wood, from which the transition is gradual. Spring tracheids squarish-hexagonal, rather



thin-walled, uniform in regular rows. Medullary rays not very numerous, resinous, prominent, and distant 2–10 rows of tracheids. Resin cells somewhat distant on the outer face of the summer wood, but readily recognizable.

*Radial.* Rays somewhat resinous throughout, the tracheids wholly marginal. Ray cells chiefly straight except in the summer wood; the upper and lower walls medium, unequal, strongly pitted, especially in the summer wood; the terminal walls strongly pitted; the lateral walls with very small, oval, bordered pits with a lenticular orifice, which soon becomes oblong and narrow, at first very variable and upwards of 5, soon uniformly 2, and in the summer wood 1, per tracheid. Bordered pits numerous, round or elliptical, in 1 row, sometimes in pairs. Pits on the tangential walls of the summer wood rather numerous and flat, not very large. Resin cells 20  $\mu$  wide, 150–275  $\mu$  long.

*Tangential.* Rays medium, resinous, the cells unequal, chiefly broad but variable, round or oval, more rarely oblong.

### 3. *T. caroliniana*, Engel.

#### *Hemlock*

*Transverse.* Growth rings medium, variable, the dense and prominent summer wood composed of rather small and more or less rounded tracheids, the transition from the spring wood rather abrupt, often quite gradual, usually much less than, or again upwards of one half, the spring wood. Spring tracheids rather large, uniform and thin-walled in regular rows, usually elongated radially. Medullary rays prominent, not very broad, 1 cell wide, distant 2–10 rows of tracheids. Resin cells on the outer face of the summer wood prominent, resinous, not very numerous, sometimes aggregated to form limited but conspicuous and irregular layers on the inner face of the summer wood.

*Radial.* Rays uniformly somewhat resinous throughout, the tracheids prominent, sometimes interspersed. Ray cells not conspicuously contracted at the ends except in the summer wood, equal to 6–8 spring tracheids, becoming much shorter in the summer wood; the upper and lower walls medium, very sparingly pitted except in the outer summer wood; the terminal walls coarsely pitted throughout; the lateral walls with small, narrowly bordered pits, the orifice at first lenticular, at length narrowly oblong, at first 2–6, finally reduced to 1, per tracheid in the summer wood. Bordered pits round or elliptical, very numerous, usually as broad as the tracheid, in 1 compact row. Pits on the tangential walls of the summer tracheids numerous but small and not very prominent. Resin cells on the outer face of the summer wood 15  $\mu$  wide, 185–310  $\mu$  long; those on the inner face very short and cylindrical, irregular and unequal, and forming a continuous series without canals.

*Tangential.* Rays rather numerous, medium, narrow, resinous, sometimes constricted by the occasional and narrow, oblong tracheids; the cells somewhat unequal, chiefly oblong but rather variable, and sometimes becoming oval.

A small tree 12–15 m. high, with a trunk .60–.75 m. in diameter.  
Wood light, soft, not strong, brittle, coarse grained.

Relative specific gravity . . . . .	0.4275
Percentage of ash residue . . . . .	0.40
Approximate relative fuel value . . . . .	42.58
Coefficient of elasticity in kilograms on millimeters . . . . .	713.
Ultimate transverse strength in kilograms . . . . .	197.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6450.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1996.
(Sargent)	

Dry, rocky ridges; rare and local at elevations of 4000–5000 feet.  
Southern Allegheny region; Bluff Mountain, Pinnacle Mountain, New River, Whitesides Mountain, and Devil's Court-House Peak, North Carolina; Saluda Mountain, Caesar's Head, South Carolina (Sargent).

#### 4. *T. Pattoniana*, Sénéc.

##### *Mountain Hemlock. Patton Spruce*

*Transverse.* Growth rings variable, chiefly rather narrow, the structure usually open throughout. Summer wood very narrow, rather open, the transition from the spring wood very gradual. Spring tracheids rather large and thin-walled, conspicuously squarish, uniform, in regular rows. Medullary rays numerous, broad, 1 cell wide, rather prominent, distant 2–7 rows of tracheids. Resin passages sometimes present though imperfectly formed, generally in a short zone on the outer face of widely distant growth rings. Resin cells on the outer face of the summer wood numerous, resinous, and prominent, sometimes aggregated to form distinct and rather broad zones. Resinous tracheids often forming small groups or radial series in contact with the rays.

*Radial.* Rays uniformly somewhat resinous throughout; the ray tracheids narrow, marginal, often locally wanting. Ray cells straight or somewhat contracted at the ends, equal to 10–15 spring tracheids; the terminal walls sparingly pitted; the upper and lower walls medium to thick, rather strongly pitted, especially in the summer wood; the lateral walls with small, oval, at first narrowly bordered pits, the lenticular orifice at length oblong, 1–4, chiefly 2, per tracheid, becoming 1 in the summer wood, where the orifice is a prolonged slit. Bordered pits round or elliptical, chiefly somewhat distant in 1 row, large, the round orifice large. Pits on the tangential walls of the summer wood not very numerous, small, often remote and obscure. Resin cells on the outer face of the summer wood 15–20  $\mu$  wide, 115–275  $\mu$  long, chiefly about 150  $\mu$ . Resinous tracheids sometimes locally numerous, the resin massive.

*Tangential.* Rays numerous, medium to high, somewhat resinous; the cells oblong-oval, more rarely oval, rather equal and uniform. Ray tracheids very few, terminal, very often wanting.

An Alpine tree rarely 30 m. in height, with a trunk 1.50–2.10 m. in diameter. Wood light, soft, not strong, close grained, satiny, susceptible of a good polish.

Relative specific gravity . . . . .	0.4454
Percentage of ash residue . . . . .	0.44
Approximate relative fuel value . . . . .	44.35
Coefficient of elasticity in kilograms on millimeters . . . . .	775.
Ultimate transverse strength in kilograms . . . . .	307.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6074.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1664.
(Sargent)	

Dry slopes and ridges near the limits of tree growth, from 2700 feet in British Columbia to 10,000 feet in Colorado.

Valley of the Fraser River, on Silver Mountain, Yale, and probably much farther north (Macoun); south along the Cascade Mountains and the California Sierras to the headwaters of the San Joaquin River; eastward along the high mountains of northern Washington to the Cœur d'Alene and Bitter Root mountains of Idaho, and the divide between Thompson and Little Bitter Root creeks in northern Montana (Sargent).

### 5. *T. Mertensiana*, Carr.

#### *Western Hemlock*

*Transverse.* Growth rings thin, the prominent summer wood dense and about equal to the spring wood, from which the transition is gradual. Spring wood very open, the large and thin-walled tracheids conspicuously squarish, in very regular rows, uniform. Medullary rays very prominent, resinous, rather broad, 1 cell wide, distant 1–9 rows of tracheids. Resin cells very prominent and resinous, sometimes forming short rows of imperfectly organized resin canals on the outer face of the summer wood.

*Radial.* Rays uniformly somewhat resinous throughout, the tracheids very unequal, short, sometimes obscure, not infrequently interspersed. Ray cells narrow, conspicuously contracted at the ends, equal to 4–9 spring tracheids; the upper and lower walls medium, unequal, rather strongly pitted; the terminal walls coarsely pitted; the lateral walls with small, conspicuously bordered oval pits with an oblong orifice, 1–2, rarely 3, per tracheid, becoming obscure in the summer wood. Bordered pits round or elliptical in 1 row. Pits on the tangential walls of the summer tracheids numerous but small and obscure. Resin canals composed of short, cylindrical resin cells, which unite to form disconnected passages. Resin cells very long and narrow, about 15  $\mu$  wide and 150–385  $\mu$  long.

*Tangential.* Rays rather numerous, medium to high, resinous, rather broad, the somewhat thick-walled cells rather unequal and variable, round or oval.

A large tree 30–61 m. high, with a trunk 1.20–3 m. in diameter.  
Wood light, hard, not strong, rather close grained.

Relative specific gravity . . . . .	0.5182
Percentage of ash residue . . . . .	0.42
Approximate relative fuel value . . . . .	51.61
Coefficient of elasticity in kilograms on millimeters . . .	1375.
Ultimate transverse strength in kilograms . . . . .	388.
Ultimate resistance to longitudinal crushing in kilograms	8747.
Resistance to indentation to 1.27 mm. in kilograms . . .	1622.

(Sargent)

Low, moist bottoms and rocky ridges; very common and reaching its greatest development in western Oregon and Washington, often forming extensive forests (Sargent); valley of the Columbia at Donald, at 1000 feet elevation, thence westward to Stony Creek at 3500 feet, thence the predominant tree to the Selkirk summit (Macoun); Alaska, thence south along the islands and coast of British Columbia and through the Rocky Mountains to the Bitter Root Mountains of Idaho; the western slopes of the Rocky Mountains of Montana; through the Cascade Mountains of southern Oregon and the coast ranges to Marin County, California, between 1000 and 4000 feet elevation (Sargent).

#### 14. \* PSEUDOTSUGA, CARR. PLATES 46 AND 47

*Transverse.* Growth rings and summer wood very variable. Resin passages prominent and well formed without thyloses, but with thick-walled epithelium. Resin cells more or less numerous on the outer face of the summer wood, not very resinous, and usually distinguished by their (1) thinner walls and somewhat advanced position, and (2) by the sieve-plate structure of the terminal walls.

*Radial.* Ray tracheids present. Ray cells with thick and coarsely pitted terminal walls. Wood tracheids always with flat and close spirals in double series.

*Tangential.* Fusiform rays present, generally narrow, the central tract composed of 1 small resin canal without thyloses, but with small and thick-walled epithelium cells; the ray cells thick-walled throughout.

#### SYNOPSIS OF SPECIES

Ray cells (tangential) distinctly oval or oblong.

Pits on the lateral walls of the ray cells small, round or oval, at first 3–7, soon 1–3, per tracheid.

##### 1. \* P. Douglasii.

Ray cells (tangential) broad, distinctly squarish, more rarely oval or round.

Pits on the lateral walls of the ray cells conspicuously larger than in 1, the orifice lenticular, 3–6 per tracheid.

##### 2. P. macrocarpa.

Ray cells oval or round (tangential).

Pits on the lateral walls of the ray cells 4 per tracheid.

3. \*\* *P. miocena*.

1. \* *P. Douglasii*, Carr.

*Yellow Fir. Oregon Pine. Douglas Fir*

*Transverse.* Growth rings very variable, and either very thin with a close, compact grain, or very broad with a coarse, open grain. Summer wood very variable, now barely distinguishable, or again upwards of one half the spring wood, often hard and flinty; transition from the spring wood more or less abrupt. Spring tracheids large, thin-walled, hexagonal, uniform in regular rows. Medullary rays prominent and somewhat resinous, rather few, 1 cell wide, distant 2-13 rows of tracheids. Resin passages rather few and widely scattering, chiefly in the summer wood, the canal equal to about 1 or 2 tracheids. Resin cells few and distant on the outer face of the summer wood, not very prominent or resinous, chiefly distinguished by their position and the sieve-plate structure of the terminal walls.

*Radial.* Rays sparingly resinous throughout, the tracheids prominent, chiefly narrow and marginal, but sometimes interspersed. Ray cells straight or somewhat contracted at the ends; the upper and lower walls thickish, irregularly and often imperfectly pitted; the terminal walls coarsely pitted; the lateral walls with small, elliptical pits, the border narrow, the orifice lenticular, at first 3-7, soon becoming 1-3, and in the summer wood 1, per tracheid. Pits on the tangential walls of the summer tracheids wanting. Resin cells 15-25  $\mu$  wide, 125-225  $\mu$  long. Bordered pits in 1 row, sometimes in pairs, generally elliptical, the orifice large. Spirals generally wanting in the summer tracheids, the angle 82°.

*Tangential.* Fusiform rays with linear and unequal terminals. Ordinary rays low to medium, the cells oval to oblong. Medullary ray cells all thick-walled.

This species presents the most striking variations of any of the North American Coniferae. These variations appear as follows:

1. The growth rings occur in zones, between which there are pronounced differences in the average thickness of the component rings (52).

2. The growth rings vary from several millimeters in thickness to less than 1 mm. In this respect a distinction may be made between the "fine-grained," in which the rings seldom exceed 2-2.5 mm., usually being much less, and the "coarse-grained" wood, in which the rings approximate to 4 mm. in thickness; the latter is further distinguished by its coarse, open grain, and often very flinty summer wood, thus approximating to the "red fir," as represented by the next species.

3. The summer wood varies greatly, either in the same tree or in different trees, being in one case barely if at all distinguishable; or, on the other hand, becoming very prominent, dark, dense and flinty, and often equal to the spring wood.

4. The size of the tracheids and the volume of the lumen vary relatively to the total area of the cross section, whereby in some cases the summer wood presents a very dense structure, while in others it is comparatively open. The extreme variations observed in nine specimens from different localities lie within the following limits:

Spring wood . . . . .	24 x 43 $\mu$ - 43 x 77 $\mu$
Summer wood . . . . .	18 x 27 $\mu$ - 26 x 53 $\mu$

A large tree 61-92 m. high, with a trunk upwards of 3.66 m. in diameter. Wood hard, strong, varying greatly with age and conditions of growth, difficult to work, very durable (Sargent).

Two varieties are recognized: the "yellow fir," distinguished by its lighter color and usually fine and compact grain; and the "red fir," which approximates to the characteristics of the next species and is distinguished by its darker red color, coarse grain, and flinty summer wood. The former is of superior quality for constructive purposes. The great strength and durability of this wood make it the most valuable species of the Pacific region, and it is largely employed where these qualities, joined to great size of timber, are required.

Relative specific gravity . . . . .	0.5157
Percentage of ash residue . . . . .	0.08
Approximate relative fuel value . . . . .	51.53
Coefficient of elasticity in kilograms on millimeters . . . . .	1283.
Ultimate transverse strength in kilograms . . . . .	376.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	8289.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1608.
(Sargent)	

A comparison of these values with those given by Sargent for some of the more commonly used oaks will serve to show the superior quality of this timber, which has a higher coefficient of elasticity than our three best native species.

COMPARATIVE STRENGTH OF OAKS AND DOUGLAS FIR  
(After Sargent)

	Coefficient of Elasticity in Kilograms on Millimeters	Ultimate Transverse Strength in Kilograms	Ultimate Resistance to Longitudinal Crushing in Kilograms	Resistance to Indentation to 1.27 mm. in Kilograms
Pseudotsuga Douglasii	1283	376	8289	1608
White oak ( <i>Quercus alba</i> )	971	386	8183	3388
Red oak ( <i>Quercus rubra</i> )	1137	422	8172	2825
Live oak ( <i>Quercus virens</i> )	1136	434	8748	5185

According to experiments reported by Dr. Bovey, as carried out in the testing laboratories at McGill University, the following values may be assigned to Douglas fir:

Specially selected wood, free from knots and cut out of the log at a distance from the heart, gave

Coefficient of bending, pounds per square inch . . . . .	9,000
Coefficient of elasticity in pounds . . . . .	2,000,000
Weight per cubic foot . . . . .	34

Ordinary first-quality wood gave

Coefficient of bending, pounds per square inch . . . . .	6,000
Coefficient of elasticity in pounds . . . . .	1,430,000
Weight per cubic foot . . . . .	34

The Douglas fir often forms extensive forests to the almost complete exclusion of other species, ranging from sea level to an elevation of nearly 10,000 feet in Colorado, and reaching its greatest development and value in Oregon and Washington (Sargent).

All parts of Vancouver Island with the exception of the exposed western coast; near the 49th parallel it ranges from the coast of the mainland to the Rocky Mountains, where it occurs in a stunted form at elevations of 6000 feet; on the eastern slopes of the Rocky Mountains, from the 49th parallel northward through the Porcupine Hills to the Bow River, where it reaches its eastern extension at Calgary; in the interior of southern British Columbia it is generally confined to the higher uplands between river valleys; northward it descends to the general level of the country (Macoun); mountain ranges of Washington, Oregon, and the California coast ranges and the Sierra Nevadas; east to Montana, Wyoming, Colorado, and the Guadeloupe Mountains of northern and eastern Arizona, and southward into Mexico (Sargent).

This tree is known but sparingly in the fossil state, the only representative so far known having been derived from the glacial deposits at Mystic Lake, near Bozeman, Montana. The age of these deposits cannot be accurately determined from the present data, but they probably represent the result of glaciation which may have continued for some time after the period of continental glaciation, and even until quite recently. The tree is, however, now extinct in that locality, and it is possible that its elimination may have been due to the same general causes that brought about a withdrawal of *Sequoia* from the prairie region during glacial time.

2. *P. macrocarpa*, Mayr.*Hemlock*

*Transverse.* Growth rings broad, variable, the dense summer wood composed of rather small, rounded tracheids in irregular rows, upwards of one third the spring wood, from which the transition is gradual. Spring tracheids rather large and squarish-hexagonal, the walls medium, rather uniform in regular rows. Medullary rays prominent and resinous, numerous and wide, chiefly 1 cell wide, distant 1-6 rows of tracheids. Resin passages numerous but scattering, equal to about 2 tracheids. Resin cells numerous and prominent on the outer face of the summer wood, and at once recognizable by their color, position, and structure. Resinous tracheids sometimes present and forming small groups or radial series in contact with the rays.

*Radial.* Rays sparingly resinous throughout, the tracheids narrow, marginal, or sometimes interspersed. Ray cells straight or contracted at the ends, equal to 6-10 spring tracheids; the upper and lower walls medium, sparingly pitted except in the summer wood; the terminal walls chiefly rather thin and not very strongly pitted; the lateral walls with prominent and resinous pits conspicuously much larger than in *P. Douglasii*, the border prominent, the orifice at first lenticular, at length oblong, at first 3-6 throughout the spring wood, somewhat abruptly reduced to 1 per tracheid in the summer wood. Bordered pits numerous in 1 row, strongly elliptical. Pits on the tangential walls of the summer tracheids few, very small and obscure. Resin cells upwards of 50  $\mu$  wide and 135-300  $\mu$  long. Spirals more or less obscure, often distant, finally vestigial and in the summer wood wanting, the angle 70°.

*Tangential.* Fusiform rays lenticular or the terminals unequally linear, narrow, the central tract with 1 small resin canal. Ordinary rays sometimes 2-seriate in part, resinous, broad, medium to high; the cells often very unequal, rather uniform, squarish, more rarely oval or round. Rays much more numerous than in *P. Douglasii*.

A tree 30-54 m. in height, with a trunk of 1.08 m. in diameter.

Wood heavy, hard, strong, cross grained, very durable, difficult to work.

Relative specific gravity . . . . .	0.4563
Percentage of ash residue . . . . .	0.08
Approximate relative fuel value . . . . .	45.59
Coefficient of elasticity in kilograms on millimeters . . . . .	1050.
Ultimate transverse strength in kilograms . . . . .	361.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7405.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1642.
(Sargent)	

Dry ridges and cañons between 2500 and 4000 feet elevation; the coast ranges of California; San Bernardino Mountains to the Cuyamaca Mountains (Sargent).



3. \*\* *P. miocena*, Penh.

*Transverse.* Growth rings broad and prominent; the tracheids of the spring wood large and thin-walled, the structure passing gradually into the thin but rather prominent summer wood composed of about 3-10 rows of thick-walled tracheids. Resin cells not obvious. Resin passages small, not very numerous, chiefly in the summer wood, often double, as in *P. Douglasii*; the epithelium cells small and thick-walled. Medullary rays slightly resinous. The entire structure of the transverse section bears a strong resemblance to the fine-grained wood of *P. Douglasii*.

*Radial.* Bordered pits in 1 row. Cells of the medullary rays straight, the thin upper and lower walls devoid of pits. Pits on the lateral walls of the ray cells about 4 per tracheid.

*Tangential.* Ordinary rays 1-seriate or 2-seriate in part, the cells oval or round, thick-walled, about  $24.5 \mu$  broad. Fusiform rays narrow, the cells thick-walled, the resin canal narrow.

Material silicified or preserved in the natural state.

Eocene of the Great Valley and Porcupine Creek groups, Saskatchewan; Miocene of Cariboo, British Columbia.

15. \* *LARIX*, TOURN. PLATES 48 AND 49

*Transverse.* Summer wood prominent, usually dense, the transition from the spring wood more or less abrupt. Resin passages without thyloses but with thick-walled epithelium. Resin cells somewhat frequent, but scattering on the outer face of the summer wood.

*Radial.* Ray tracheids prominent, sometimes interspersed; the terminal walls of the parenchyma ray cells thick and strongly pitted. Bordered pits in 1 or 2 rows. Tracheids wholly without spirals.

*Tangential.* Fusiform rays prominent, usually high and narrow, the cells small and thick-walled, the resin passage usually small. Cells of the ordinary rays oval to oblong.

A well-defined genus, at once distinguished by the narrow and usually high fusiform rays, the resin cells scattering on the outer face of the summer wood, and the absence of spiral tracheids.

## SYNOPSIS OF SPECIES

Bordered pits in 1-2 rows.

Pits on the tangential walls of the summer wood not confined to the outermost tracheids.

Pits on the lateral walls of the ray cells 2-6 or 8 per tracheid.

Ray cells (tangential) rather unequal, sometimes in pairs, somewhat variable, oval or oblong.

1. *L. occidentalis*.

Pits on the tangential walls of the summer wood confined to the outermost tracheid.

Pits on the lateral walls of the ray cells 2-6 per tracheid.

Ray cells (tangential) equal, uniform, and oblong, more rarely oval.

2. \* *L. americana*.

Bordered pits in 1 row, sometimes in pairs.

Pits on the tangential walls of the summer wood confined to the outermost tracheid.

Pits on the lateral walls of the ray cells 3-6; those on the tangential walls of the summer wood numerous and small.

Ray cells (tangential) equal and very uniform, narrowly oblong.

3. *L. Lyallii*.

Pits on the lateral walls of the ray cells 2-6 per tracheid; those on the tangential walls of the summer wood few, small, confined to the outermost wall.

Ray cells (tangential) oblong, more rarely oval, and much broader.

4. *L. leptolepis*.

### 1. *L. occidentalis*, Nutt.

#### *Tamarack*

*Transverse.* Growth rings usually broad, the dense and prominent summer wood about one half the spring wood, from which the transition is abrupt. Tracheids of the summer wood large, squarish, in regular rows. Tracheids of the spring wood very large and thin-walled, squarish-hexagonal, in very regular rows, rather uniform. Medullary rays prominent, rather resinous and broad, 1 cell wide, distant 2-6 rows of tracheids. Resin passages few, large, without thyloses, the epithelium narrow, rather thin-walled, the nutritive layer thick-walled, resinous. Resin cells widely scattering on the outer face of the summer wood, but readily recognized by their abundant resinous contents.

*Radial.* Rays conspicuously resinous throughout; the tracheids narrow and marginal, rarely interspersed. Ray cells chiefly straight throughout and equal to 3-9 spring tracheids; the upper and lower walls chiefly thick and unequal, sparingly pitted throughout, more strongly so in the summer wood; the terminal walls coarsely pitted throughout; the lateral walls with elliptical and distinctly bordered pits, with a narrow, chiefly oblong or lenticular orifice, numerous, at first 6-8 per tracheid, soon greatly reduced in size, and in the summer wood abruptly 1 per tracheid. Bordered pits conspicuously in 1-2 rows, more rarely in 1 row only, elliptical, the orifice very large. Pits on the tangential walls of the summer wood rather numerous but small and often obscure. Resin cells about 12.5  $\mu$  wide and 60-150  $\mu$  long.

*Tangential.* Rays rather numerous, low to very high. Fusiform rays with a large resin canal without thyloses, the epithelium cells thick-walled. Ordinary rays often very high, chiefly very uniform, and not contracted at the position of the rarely interspersed tracheids; the parenchyma cells rather unequal, sometimes in pairs, oval or oblong, somewhat variable.

This species appears to be more or less variable according to local conditions of growth. From low elevations specimens appear to exhibit little variation, but from high elevations (Mt. Higgins, Montana, altitude 8700 feet) they present very well-defined structural deviations. These appear chiefly in the much narrower and unequal growth rings.

A tree 30-45 m. high, with a trunk upward of 1.50 m. in diameter.

Wood heavy, exceedingly hard and strong, rather coarse grained, compact, satiny, susceptible of a fine polish, very durable in contact with the soil, and of great economic value.

Relative specific gravity . . . . .	0.7407
Percentage of ash residue . . . . .	0.09
Approximate relative fuel value . . . . .	74.
Coefficient of elasticity in kilograms on millimeters . . .	1658.
Ultimate transverse strength in kilograms . . . . .	524.
Ultimate resistance to longitudinal crushing in kilograms	11,023.
Resistance to indentation to 1.27 mm. in kilograms . . .	2395.
(Sargent)	

Abundant in the Kootenai-Columbia valley of British Columbia (Macoun); through the mountain ranges of northern Washington to the western slopes of the Rocky Mountains of Montana; the Blue Mountains of Washington and Oregon; moist mountain slopes and benches between 2500 and 5000 feet elevation; scattered among other trees, never forming separate forests (Sargent).

## 2. *L. americana*, Michx.

*Larch. Black Larch. Tamarack. Hackmatack*

*Transverse.* Growth rings rather broad and uniform, sometimes double. Summer wood rather dense, about one fourth to one half the spring wood, from which the transition is either gradual or abrupt, the tracheids small, conspicuously unequal and not in very regular rows, distinctly rounded. Spring tracheids large, hexagonal, radially elongated, thin. Medullary rays prominent, broad, 1 cell wide, distant 2-8, rarely more, tracheids. Resin passages large, equal to 2-3 tracheids, devoid of thyloses; the epithelium cells flat, rather thin-walled; the nutritive parenchyma scanty, thick-walled; not very numerous, chiefly in the summer wood. Resin cells few, widely scattering on the outer face of the summer wood, nonresinous, distinguished by (1) their thinner walls and advanced position, and (2) by the sieve-plate structure of the terminal walls.

*Radial.* Rays somewhat resinous throughout; the tracheids prominent, numerous, and marginal. Parenchyma ray cells straight or barely contracted in the summer wood; the upper and lower walls thick, unequal, and usually sparingly pitted; the terminal walls coarsely pitted throughout; the lateral walls with distinctly bordered pits, the narrow orifice chiefly oblong, 2-6 per tracheid, becoming distinctly smaller toward the summer wood, where they are abruptly reduced to 2, and finally 1, per tracheid. Bordered pits in 1 or 2 rows, large, elliptical, becoming smaller and round toward the summer wood. Pits often showing an equatorial band. Pits on the tangential walls of the summer wood numerous, small, approximate, on the outermost tracheids only. The outer summer tracheids often show a marked tendency to the formation of spirals. Resin cells 15  $\mu$  wide, about 125  $\mu$  long.

*Tangential.* Rays numerous, medium to high, sparingly resinous. The fusiform rays with a broad central tract and a large resin canal without thyloses. The ordinary rays rather broad, sometimes 2-seriate in part; the cells thick-walled, chiefly rather equal, uniform, oblong, more rarely oval. Rays somewhat contracted at the position of the narrow and interspersed tracheids.

A tree 24-30 m. high, with a trunk upwards of .90 m. in diameter. Wood heavy, hard, very strong, rather coarse grained, compact, durable in contact with the soil.

Relative specific gravity . . . . .	0.6236
Percentage of ash residue . . . . .	0.33
Approximate relative fuel value . . . . .	62.16
Coefficient of elasticity in kilograms on millimeters . . .	1261.
Ultimate transverse strength in kilograms . . . . .	384.
Ultimate resistance to longitudinal crushing in kilograms	8763.
Resistance to indentation to 1.27 mm. in kilograms . . .	1675.
(Sargent)	

Cold, wet swamps, often covering extensive areas, or northward on moist uplands and intervale lands. This tree, together with the black spruce, dominates nearly all the swampy land from Newfoundland, Labrador, and the eastern provinces of Canada to the Rocky Mountains; northward to latitude 65°, where it is reduced to a height of 6-8 feet (Macoun); southward through the northern United States to northern Pennsylvania, northern Indiana, Illinois, and central Minnesota (Sargent).

A well-defined, widely distributed, and common tree in the Pleistocene and more recent deposits, where the remains are preserved in a natural state, and often most perfectly.

Leda clays, Montreal; Scarborough Heights, Ontario; Moose River, Ontario; Lower Till of Fort Madison, Iowa; Ithaca, New York; Don Valley, Toronto; the black clays of the Columbian Formation (equivalent to Pleistocene of northern localities) at Dahlonga, Georgia; peat bogs of New Brunswick.

3. *L. Lyallii*, Parl.*Tamarack. Mountain Larch*

*Transverse.* Growth rings narrow, variable. The summer wood prominent and dense or sometimes open, equal to about one half to one third the spring wood; the tracheids in regular rows, very unequal, small, radially narrow and rounded. Spring tracheids rather large, squarish-hexagonal, thin-walled, very uniform in regular rows. Medullary rays prominent, not very broad, 1 cell wide, distant 2-8 rows of tracheids. Resin canals not very numerous, small and widely scattering, devoid of thyloses, the epithelium not very narrow, thick-walled, the nutrient parenchyma obscure or wanting. Resin cells somewhat numerous, slightly resinous and easily distinguished.

*Radial.* Rays sparingly resinous throughout, the tracheids rather numerous, marginal, sometimes interspersed. Ray cells very straight throughout, equal to 3-7 spring tracheids; the upper and lower walls thick, somewhat conspicuously pitted; the terminal walls coarsely pitted throughout; the lateral walls with numerous small, oval, distinctly bordered pits with an oblong, narrow orifice, 3-6 per tracheid, in the summer wood abruptly reduced to 1. Bordered pits in 1 row, often in pairs, elliptical, large. Pits on the tangential walls of the summer wood rather numerous but small, and confined to the outermost tracheid wall. Resin cells few, 15  $\mu$  wide, 110-155  $\mu$ , chiefly about 125  $\mu$  long.

*Tangential.* Rays rather numerous, low to high, somewhat resinous. Fusiform rays very narrow and variable in height; the narrow and linear terminals often very unequal; the cells all thick-walled; the resin canal small, usually narrow and oblong, often much reduced and nearly obliterated. Ordinary rays more or less 2-seriate in part, narrow, the cells very equal and uniform, narrowly oblong.

A low, straggling, Alpine tree, rarely exceeding 15 m. in height, with a trunk upwards of 1.50 m. in diameter.

In the Rocky Mountains of Washington and Montana (Sargent); summit of South Kootenai Pass; from Cascade Mountain, Bow River Valley, westward; forming the last belt of timber on all the peaks of the Rocky Mountains, and ranging from 6000 to 7000 feet elevation; growing with *Pinus albicaulis* (Macoun).

4. *L. leptolepis*, Gordon*Jap. = Fugimatsu*

*Transverse.* Growth rings rather broad. The very prominent and dense summer wood composed of very angular and unequal tracheids in irregular rows; nearly equal to the spring wood, from which the transition is abrupt. Spring tracheids large, thin-walled, very uniform in regular rows. Medullary rays prominent, 1 cell wide, distant 2-10 rows of tracheids. Resin passages not numerous, somewhat widely scattering, chiefly in the summer wood, the epithelium rather thin-walled,

the nutritive parenchyma thick-walled; equal to 1-2 tracheids, devoid of thyloses. Resin cells on the outer face of the summer wood few, distant; recognized by their thin walls and more advanced position, and the sieve-plate structure of the terminal walls.

*Radial.* Rays somewhat resinous throughout, with prominent, chiefly narrow, but often numerous, marginal tracheids, rarely interspersed. Ray cells conspicuously straight throughout; the upper and lower walls rather thick, at first rather sparingly, but in the summer wood very strongly, pitted; the terminal walls coarsely pitted throughout; the lateral walls with rather small, oval, bordered pits, with a lenticular orifice, 2-6, abruptly reduced to 1, per tracheid in the summer wood. Bordered pits very large, with a large oval orifice, elliptical, numerous, and often compact, two thirds the width of the tracheid, in 1 row. Pits on the tangential walls of the summer wood few, small, confined to the outermost tracheid wall. Resin cells 15  $\mu$  wide, 110-265  $\mu$  long, chiefly about 125  $\mu$ .

*Tangential.* Rays rather numerous and resinous. The fusiform rays narrow, the canal small without thyloses, the epithelium rather thick-walled. Ordinary rays medium to high, contracted at the position of the interspersed tracheids; the parenchyma cells chiefly equal and uniform, oblong, more rarely oval and broader.

#### 16. \* PICEA, LINK. PLATES 50 AND 51

*Transverse.* Growth rings variable, the transition to the usually prominent summer wood gradual. Resin passages with or without thyloses, but with thick-walled epithelium cells. Resin cells wholly wanting.

*Radial.* Ray tracheids conspicuous, chiefly narrow, marginal, or sometimes interspersed. Terminal walls of the ray cells usually strongly pitted. Tracheids wholly without spirals.

*Tangential.* Fusiform rays chiefly narrow, with linear and often very unequal and much-prolonged terminals; the cells small and thick-walled; the central tract of 1 small resin passage without thyloses but with thick-walled epithelium. Cells of the ordinary rays oblong, more rarely oval.

This genus is readily distinguished from *Larix* and *Pseudotsuga* by the absence of resin cells and of spiral tracheids.

#### SYNOPSIS OF SPECIES

Ray cells (tangential) variable, round, oval, or oblong.

Pits on the tangential walls of the summer wood chiefly or wholly confined to the outermost wall.

Pits on the lateral walls of the ray cells 1-3 per tracheid.

Ray cells (tangential) equal.

Spring tracheids rounded-hexagonal, the structure not very open.

10. *P. sitchensis*.

Pits on the tangential walls of the summer wood few, often widely scattering and extending for some distance into the summer wood.

Pits on the lateral walls of the ray cells 2-6, chiefly 4, per tracheid.

Ray cells (tangential) conspicuously unequal.

Spring tracheids large, thin-walled, uniform in regular rows, squarish-hexagonal.

6. *P. polita*.

Ray cells (tangential) usually very equal and uniform, oblong or oval.

Pits on the tangential walls of the summer wood chiefly or wholly confined to the outermost tracheid wall.

Pits on the lateral walls of the ray cells 2-4 per tracheid.

7. *P. bicolor*.

Pits on the lateral walls of the ray cells 2-6 per tracheid.

3. \* *P. alba*.

Pits on the tangential walls of the summer wood not confined to the outermost wall, but chiefly small and inconspicuous.

Rays (radial) nonresinous.

Pits on the lateral walls of the ray cells at first narrowly bordered, 2-5 per tracheid, in the summer wood reduced to 1.

Ray cells (tangential) rather thick-walled.

Spring tracheids rounded-hexagonal; the summer wood rather open but prominent, upwards of one half the spring wood.

4. *P. Engelmanni*.

Pits on the lateral walls of the ray cells with an oblong orifice, 2-6 per tracheid, toward the summer wood reduced to 2, and finally to 1.

Ray cells (tangential) thin-walled.

Spring tracheids hexagonal, very thin-walled; the summer wood very thin and open, often barely distinguishable.

8. *P. pungens*.

Rays (radial) locally resinous, the resin chiefly confined to the thicker-walled and more strongly pitted cells, more rarely diffused throughout the central cells.

Pits on the lateral walls of the ray cells with a lenticular orifice, at first 2-6 per tracheid, more rarely 2 throughout, in the summer wood reduced to 2, and finally to 1.

Spring tracheids squarish-hexagonal, not very uniform, the walls rather thin.

9. \* *P. nigra*.

Pits on the lateral walls of the ray cells with an oblong, narrow orifice, 3-5 per tracheid, in the summer wood reduced to 2, and finally to 1.

Spring tracheids large, squarish-hexagonal, very unequal in regular rows, the walls thin.

5. *P. jesoënsis*.

Pits on the lateral walls of the ray cells with a narrow, oblong orifice, at first sometimes upwards of 7 per tracheid, soon 2-4, and in the summer wood 1-2.

Spring tracheids large, squarish, very uniform in regular rows, the walls rather thin.

2. *P. rubra*.

Pits on the lateral walls of the ray cells with a narrow, oblong orifice, becoming much extended in the summer wood; 2-3, more rarely 4, per tracheid, becoming 1 in the summer wood.

Spring tracheids distinctly hexagonal, conspicuously unequal in regular rows, the walls not very thin.

1. *P. Breweriana*.

1. *P. Breweriana*, Wats.

*Weeping Spruce*

*Transverse*. Growth rings rather thin and uniform. Summer wood rather thin, of about 10-16 tracheids, prominent, not very dense, the transition from the spring wood gradual; the tracheids unequal, in rather regular rows, usually much compressed. Spring tracheids distinctly hexagonal, conspicuously unequal, in regular rows, the walls not very thin. Resin passages rather numerous, scattering, often in small groups, and more or less imperfectly formed; the epithelium in 1-2 rows of very variable but thick-walled, often resinous, cells. Medullary rays prominent, resinous, distant 2-8, more rarely 12, rows of tracheids.

*Radial*. Rays sparingly resinous; the ray tracheids marginal. Ray cells straight or becoming fusiform in the summer wood, equal to 6-7 spring tracheids; the terminal walls coarsely pitted; the upper and lower walls rather thick, unequal, more or less obscurely pitted except in the summer wood; the lateral walls with conspicuously bordered, round, or oval pits, with an oblong orifice which becomes much extended in the summer wood, 2-3, more rarely 4, per tracheid, becoming 1 in the summer wood. Bordered pits numerous, often much crowded, in 1 row, elliptical. Pits on the tangential walls of the summer wood rather numerous, not confined to the outermost tracheid wall.

*Tangential*. Rays numerous, somewhat resinous, medium to high, not very broad; the cells chiefly equal and uniform, oblong, or more rarely oval. Fusiform rays rather few, narrow; the terminals often much prolonged.



A tree upwards of 30 m., or more rarely 36 m. in height, with a trunk .60-.90 m. in diameter.

Wood soft, close grained, compact, with a satiny surface.

Relative specific gravity . . . . . 0.5141  
(Sargent)

This tree occurs in small, scattered groves in the elevated mountain regions of California and Oregon, between 4000 and 7500 feet altitude (Sargent).

## 2. *P. rubra*, Dietr.

### *Red Spruce*

*Transverse.* Growth rings narrow, rather variable. Summer wood narrow, not very prominent, upwards of 10 tracheids, rather open; the transition from the spring wood gradual. Spring tracheids rather large, not very thin-walled, in very regular rows and very uniform, squarish. Resin passages widely scattering, not numerous, medium and equal to about 2 tracheids; the epithelium composed of rather small, thick-walled cells; wholly devoid of tyloses. Resin cells wholly wanting. Medullary rays 1 cell wide, not numerous or prominent, distant 3-14 rows of tracheids.

*Radial.* Rays sparingly resinous, the resin usually localized and more or less confined to the thicker-walled and more strongly pitted cells; the ray tracheids prominent, marginal, rarely interspersed. Ray cells straight throughout, or barely fusiform in the summer wood, equal to about 5-7 spring tracheids; the terminal walls strongly pitted; the upper and lower walls rather thin, distantly and obscurely pitted, or in the summer wood more or less strongly pitted; the lateral walls with small, elliptical, bordered pits with an oblong orifice, at first sometimes upwards of 7 per tracheid, soon 2-4, and in the summer wood 1-2. Bordered pits broadly elliptical or round, in 1 row, not crowded, but variable in size. Pits on the tangential walls of the summer wood very small and much compressed.

*Tangential.* Rays somewhat numerous, medium, sparingly resinous. Fusiform rays narrow, the resin canal small with thick-walled epithelium. Ordinary rays not broad, medium, the cells very equal and uniform, oblong, or sometimes oval throughout.

A tree usually 21-24 m., and occasionally 30-33 m. in height, with a trunk .60-.90 m. in diameter.

Valley of the St. Lawrence and the northern shores of Prince Edward Island, southward through Quebec, the Maritime Provinces, and along the Atlantic coast to southern Maine and Cape Cod; through the hilly interior and the mountainous parts of New England and New York, thence along the Allegheny Mountains to the high peaks of western North Carolina (Sargent).

3. \* *P. alba*, Ait.

*White Spruce*

**Transverse.** Growth rings thick. Summer wood thin, rather prominent, upwards of one fourth the spring wood from which the transition is gradual, rarely abrupt; the structure rather dense; the tracheids conspicuously squarish. Spring wood open, the tracheids squarish-hexagonal, uniform in very regular rows, the walls thin. Resin passages scattering, rather large, round, commonly without thyloses, equal to 2-3 tracheids; the epithelium of very unequal, chiefly narrow, and rather thin-walled cells. Medullary rays not very numerous, rather prominent, narrow, 1 cell wide, distant 2-14 rows of tracheids.

**Radial.** Rays very sparingly resinous; the ray tracheids prominent, marginal, sometimes interspersed in the higher rays. Ray cells straight throughout, equal to 5-13 spring tracheids; the terminal walls coarsely pitted; the upper and lower walls rather thin, unequal, sparingly pitted in the spring wood, strongly pitted in the summer wood; the lateral walls with numerous small, oval pits with a lenticular orifice, 2-6 per tracheid, in the summer wood abruptly reduced to 2, and finally to 1. Bordered pits in 1 row, numerous, round, or elliptical, the orifice large; in the summer wood becoming remote and finally obscure, the orifice usually a prolonged slit. Pits on the tangential walls of the summer wood very flat and obscure, chiefly confined to the outermost tracheid wall.

**Tangential.** Rays rather numerous, nonresinous, low to high. Fusiform rays narrow, the cells thin-walled, the resin canal small, the epithelium composed of thick-walled cells. Ordinary rays narrow, not conspicuously contracted by the occasionally interspersed tracheids; the cells very equal and uniform, oblong, narrow.

A tree 15-50 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, soft, not strong, close and straight grained, compact, satiny.

Relative specific gravity . . . . .	0.4051
Percentage of ash residue . . . . .	0.32
Approximate relative fuel value . . . . .	40.38
Coefficient of elasticity in kilograms on millimeters . . . . .	1023.
Ultimate transverse strength in kilograms . . . . .	319.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5489.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1117.
(Sargent)	

According to Bovey the following data have been obtained:

Coefficient of strength in pounds for:

Bending . . . . .	5000
Torsion . . . . .	9000
Compression . . . . .	3200
Shear . . . . .	360
Weight of 1 cubic foot . . . . .	30

Newfoundland, Anticosti, Nova Scotia, and New Brunswick, westward through Quebec and Ontario to the forest limit of Manitoba; in the

prairie region being found in the sand hills bordering the first prairie steppe. Occasionally in the valley of the Saskatchewan and on the Bow River from Calgary, where it is mixed with *P. Engelmanni*; on the Athabasca to latitude  $54^{\circ} 7' 34''$  (Macoun). Coast of Maine through northeastern Vermont and westward through northern Michigan and Minnesota to the Black Hills of Dakota; along the Rocky Mountains of Montana, where it reaches its greatest development along streams and lakes in the Flathead region, at elevations of 2500–3500 feet (Sargent). Pleistocene of the Scarborough period of which it is characteristic, at Scarborough Heights, Ontario.

Material preserved in the natural state, but showing the effects of extensive decay.

#### 4. *P. Engelmanni*, Engelm.

*White Spruce. Engelmann's Spruce*

*Transverse.* Growth rings broad. Summer wood very prominent and rather open, about one half to one third the spring wood, from which the transition is gradual; the tracheids often much compressed radially. Spring tracheids rounded-hexagonal, unequal in regular rows, the walls thin. Resin passages without thyloses, not very numerous; the epithelium cells very unequal, rather thin-walled. Medullary rays not very prominent, narrow, 1 cell wide, distant 2–7 rows of tracheids.

*Radial.* Rays nonresinous; the ray tracheids prominent, marginal. The ray cells generally straight and equal to 7 spring tracheids; the terminal walls strongly pitted; the upper and lower walls medium and sparingly pitted, except in the summer wood; the lateral walls with small, oval, and at first narrowly bordered pits, 2–5 per tracheid, in the summer wood gradually reduced to 1. Bordered pits in 1 row, large, not very numerous, round or elliptical, the orifice finally becoming a prolonged slit upwards of  $34\ \mu$ . Pits on the tangential walls of the summer wood small and not prominent, chiefly confined to the outermost wall.

*Tangential.* Rays rather numerous, medium to high, nonresinous. The fusiform rays rather broad, the resin canal large and round, with thick-walled epithelium. The ordinary rays rather narrow, the cells very equal and uniform, narrowly oblong, rarely broader.

A large tree 24–26 m. high, with a trunk upwards of 1.20 m. in diameter. Wood very light, soft, not strong, very close and straight grained, compact, satiny.

Relative specific gravity . . . . .	0.3449
Percentage of ash residue . . . . .	0.32
Approximate relative fuel value . . . . .	33.38
Coefficient of elasticity in kilograms on millimeters . . . . .	808.
Ultimate transverse strength in kilograms . . . . .	245.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4271.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1217.
(Sargent)	

This tree characterizes the interior plateau of British Columbia, with the exception of the dry southern portions, forming dense groves in the mountains. It ranges northward to latitude  $54^{\circ} 7' 34''$  at an altitude of 2600 feet (Macoun). Dry gravelly ridges and slopes between 5000 and 11,500 feet elevation, constituting the most valuable timber tree of the central Rocky Mountains, where it forms extensive forests, generally above 8500 feet elevation. Rare and of small size in the mountains of Washington, Oregon, and Montana (Sargent).

5. *P. jesoënsis*, Carr.

*Jap.* = *Tôhi*

*Transverse.* Growth rings narrow, uniform. The very thin summer wood open and composed of 5-10 tracheids, about one fourth the spring wood, from which the transition is rather gradual. Spring tracheids large, squarish-hexagonal, thin-walled, very unequal but in regular rows. Resin passages not very numerous, chiefly large, with thyloses, the epithelium of very unequal, rather thick-walled cells. Medullary rays not numerous, rather resinous and prominent, 1 cell wide, distant 2-8 rows of tracheids.

*Radial.* Rays sparingly and locally resinous; the ray tracheids prominent and often interspersed. Ray cells somewhat contracted at the ends, equal to 3-7 spring tracheids; the terminal walls coarsely pitted; the upper and lower walls not very thick, conspicuously pitted, especially in the summer wood; the lateral walls with small, oval, bordered pits with a narrow orifice, 3-5 per tracheid, in the summer wood reduced to 2, and finally to 1. Bordered pits large, strongly elliptical, in 1 row, rather numerous, often in compact rows towards the ends of tracheids. Pits on the tangential walls of the summer wood rather few, small, and inconspicuous.

*Tangential.* Rays not very numerous, low to medium, sparingly resinous. Fusiform rays rather broad, the rather large resin canal with thick-walled epithelium, chiefly without thyloses. Ordinary rays not very broad, contracted at the position of the sparingly interspersed tracheids; the cells rather thick-walled, very equal and uniform, narrowly oblong, rarely oval.

6. *P. polita*, Carr.

*Jap.* = *Iramomi*

*Transverse.* Growth rings thin, very variable. Summer wood prominent, rather dense but variable, from 3 tracheids thick upwards, equal to one half to one third the spring wood from which the transition is rather gradual; the tracheids variable. Spring tracheids rather large and thin-walled, uniform in regular rows. Resin passages rather numerous, large but variable, equal to 1-4 tracheids, with thyloses; the epithelium of very unequal, rather thin-walled cells. Medullary rays rather numerous and broad, 1 cell wide, resinous, distant 2-8 or 10 rows of tracheids.

*Radial.* Rays locally very resinous throughout; the ray tracheids low, unequal, marginal, sometimes interspersed. Ray cells more or less contracted at the ends, especially in the summer wood, equal to 7-8 spring tracheids; the terminal walls thin, often locally thickened or sparingly pitted, sometimes entire; the upper and lower walls thicker and strongly pitted in the resinous cells, thinner and sparingly pitted in the nonresinous cells; the lateral walls with small, oval, bordered pits, the orifice narrow, oblong, 2-6, chiefly 4, per tracheid, in the summer wood rather abruptly reduced to 1. Bordered pits numerous, elliptical, in 1 row, sometimes in pairs. Pits on the tangential walls of the summer wood rather few and not very prominent, flat, often widely scattering, and extending for some distance into the summer wood.

*Tangential.* Rays numerous, low to high, rather broad, resinous. The fusiform rays rather narrow, with a small resin canal and thick-walled epithelium. Ordinary rays contracted at the position of the occasionally interspersed and very narrow tracheids; the parenchyma cells conspicuously unequal and variable, from round or oval to oblong, often narrow and high.

#### 7. *P. bicolor*, Mayr.

*Jap.* = *Ô-Tôhi*

*Transverse.* Growth rings narrow, uniform. The narrow summer wood of 6-10 tracheids, about equal to one third to one half the spring wood from which the transition is rather gradual; not very dense, the tracheids much flattened and rounded. Spring tracheids conspicuously squarish, thin-walled, uniform in very regular rows. Resin passages rather large, often with thyloses; the epithelium composed of very unequal, thick-walled cells. Medullary rays rather prominent, somewhat resinous, 1 cell wide, distant 2-10 rows of tracheids.

*Radial.* Rays somewhat resinous, the resin localized; the ray tracheids numerous, prominent, and marginal, often interspersed. Parenchyma cells straight, equal to about 8 tracheids; the terminal walls thin, at first sparingly, soon strongly, pitted throughout; the upper and lower walls medium, very sparingly pitted, or again thicker and strongly pitted, especially in the summer wood; the lateral walls with small, elliptical, bordered pits, with an oblong orifice, 2-4 per tracheid, abruptly reduced to 1 in the summer wood. Bordered pits large, elliptical, or round, in 1 row. Pits on the tangential walls of the summer wood not very numerous, small, chiefly confined to the outermost wall.

*Tangential.* Rays rather numerous but low to medium, somewhat resinous. The fusiform rays chiefly low, narrow, the usually small resin canal with thick-walled epithelium. Ordinary rays conspicuously contracted at the position of the very narrow, interspersed tracheids; the parenchyma cells thick-walled, equal and chiefly uniform, oblong, often narrow, rarely oval.

8. *P. pungens*, Engelm.

*Blue Spruce. Colorado Spruce*

*Transverse.* Growth rings broad. The very thin and often barely distinguishable summer wood gradually passing into the spring wood; the tracheids very unequal and often much compressed radially. Spring tracheids hexagonal, very thin-walled, uniform in regular rows. The structure is very open throughout. Resin passages rather few, small, and scattering, with small and very unequal, thick-walled epithelium cells; thyloses few or wanting. Medullary rays rather numerous and broad, 1 cell wide, distant 2-9 rows of tracheids.

*Radial.* Rays nonresinous; the ray tracheids numerous and marginal, rarely interspersed. Parenchyma cells chiefly straight, equal to about 7 spring tracheids; the terminal walls coarsely pitted; the upper and lower walls medium and entire or conspicuously pitted throughout; the lateral walls with small, oval, bordered pits with an oblong orifice, 2-6 per tracheid, toward the summer wood reduced to 2, and finally to 1. Bordered pits numerous, in 1 row, elliptical or round; the round orifice becoming lenticular in the summer wood. Pits on the tangential walls of the summer wood small, not numerous or prominent, chiefly confined to the outermost walls.

*Tangential.* Rays numerous, nonresinous, medium to high. The fusiform rays narrow, the resin canal rather small, with thick-walled epithelium. The ordinary rays contracted at the position of the occasionally interspersed tracheids; the parenchyma cells rather thin-walled, very equal and uniform, oblong, rather narrow.

A tree 30-46 m. high, with a trunk upwards of .90 m. in diameter.

Wood very light, soft, weak, close grained, compact, satiny.

Relative specific gravity . . . . .	0.3740
Percentage of ash residue . . . . .	0.38
Approximate relative fuel value . . . . .	37.26
Coefficient of elasticity in kilograms on millimeters . . . . .	553.
Ultimate transverse strength in kilograms . . . . .	194.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4128.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1267.

(Sargent)

Along borders of streams in damp or wet soil, generally between 6000 and 9000 feet elevation, and never forming forests. Rare and local. Valley of the Wind River and south through the mountains of Wyoming, Colorado, and Utah (Sargent).

9. \* *P. nigra*, Ait.

*Black Spruce*

*Transverse.* Growth rings rather broad, variable. The summer wood usually much less than but upwards of one half the spring wood, from which the transition is gradual; the structure open. Spring tracheids squarish-hexagonal, not very uniform, in regular rows, the walls rather thin. Resin passages chiefly in the summer wood, equal to 2-4

tracheids with thyloses; the epithelium cells very much flattened, rather thin-walled. Medullary rays rather prominent, 1 cell wide, rather numerous, distant 2-8 rows of tracheids.

**Radial.** Rays very sparingly resinous; the ray tracheids prominent, marginal, sometimes interspersed. Parenchyma cells straight or rarely narrower at the ends, long; the terminal walls coarsely pitted; the upper and lower walls medium, sinuately unequal, distantly and often obscurely pitted except in the summer wood; the lateral walls with small, oval, bordered pits with a lenticular orifice, 2-6 per tracheid, more rarely 2 throughout, in the summer wood reduced to 2, and finally to 1. Bordered pits numerous, crowded, *round*, or elliptical, the orifice large, round, becoming narrow in the summer wood and parallel with the tracheid axis. Pits on the tangential walls of the summer wood very narrow and small, but generally numerous.

**Tangential.** Fusiform rays very narrow and high; the cells small and thick-walled; the terminals very long and linear, often unequal; the resin canal rather small and narrow, oblong. Ordinary rays very narrow, the cells very equal and uniform, oblong and narrow at least in the higher rays, more rarely rather broad and oval.

A tree 15-21 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, soft, not strong, close and straight grained, compact, satiny.

Relative specific gravity . . . . .	0.4594
Percentage of ash residue . . . . .	0.27
Approximate relative fuel value . . . . .	45.71
Coefficient of elasticity in kilograms on millimeters . . . . .	1100.
Ultimate transverse strength in kilograms . . . . .	318.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6520.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1240.

(Sargent)

Abundant in Newfoundland and in every part of Canada except southern Ontario and the prairie region, ranging northward to latitude 65°, where it terminates in association with *Betula papyrifera* (Macoun). Through the northern United States to Pennsylvania, central Michigan, Wisconsin, and Minnesota, and along the Allegheny Mountains to the high peaks of North Carolina (Sargent).

Pleistocene deposits at Hamilton (Erie clays), Ontario; the Moose River, Ontario; Don Valley and the Leda Clays, Montreal. This plant occurs in considerable abundance and is essentially typical of the Don period, where it is associated with another undescribed species, possibly the same.

Material preserved in a natural state, though usually much altered by decay.

#### 10. *P. sitchensis*, Carr.

*Tideland Spruce. Sitka Spruce*

**Transverse.** Growth rings thickish. Summer wood very prominent, equal to or exceeding the spring wood from which the transition is gradual, not very dense. Spring tracheids commonly strongly rounded-hexagonal,

the walls rather thin, but the structure as a whole not very open. Resin passages few, not very large, with thyloses; the epithelium of small, thick-walled cells, resinous. Medullary rays not very numerous, prominent or broad, 1 cell wide, distant 2-9 rows of tracheids, more rarely 11.

*Radial.* Rays somewhat resinous locally; the ray tracheids prominent, marginal, rarely interspersed. Parenchyma cells somewhat contracted at the ends, equal to 6-10 spring tracheids; the terminal walls coarsely pitted; the upper and lower walls medium or thin and entire, or in the resinous cells and summer wood becoming thicker and pitted; the lateral walls with rather few and small, narrowly bordered pits with a lenticular orifice, 1-3, more rarely 4, per tracheid, in the summer wood reduced to 2, and finally to 1. Bordered pits in 1 row, elliptical, large; the orifice large and round or lenticular, in the summer wood becoming narrow and parallel with the tracheid axis. Pits on the tangential walls of the summer wood few, small, and chiefly or wholly confined to the outermost tracheid wall.

*Tangential.* Rays medium to high, somewhat resinous. The fusiform rays narrow, the resin canal small, with small and thick-walled epithelium cells. Ordinary rays rather broad, conspicuously contracted at the position of the narrow and occasionally interspersed tracheids; the parenchyma cells equal but variable from round to oval or oblong.

A large tree of great economic value, 46-61 m. high, with a trunk 2.40-5.19 m. in diameter.

Wood light, soft, not strong, close and straight grained, compact, satiny.

Relative specific gravity . . . . .	0.4287
Percentage of ash residue . . . . .	0.17
Approximate relative fuel value . . . . .	42.80
Coefficient of elasticity in kilograms on millimeters . . . . .	990.
Ultimate transverse strength in kilograms . . . . .	277.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5653.
Resistance to longitudinal crushing to 1.27 mm. in kilograms . . . . .	1160.

(Sargent)

Chiefly confined to the coast of British Columbia, where it attains large size (Macoun); Alaska, south to Mendocino County, California, not extending more than 50 miles inland from the coast (Sargent).

## 17. \* PINUS, TOURN.

*Transverse.* Growth rings usually broad. The more or less prominent summer wood variable. Resin passages prominent, chiefly large, with prominent thyloses and thin-walled, variable, several-layered epithelium. Resin cells wholly wanting.

*Radial.* Ray tracheids prominent and always limiting the ray, often interspersed, sometimes predominant, and in rays only a few elements high, commonly constituting the entire structure; the upper and lower walls often dentate (Sec. II), the teeth sometimes united across the tracheid so as to form more or less prominent reticulations. Ray cells



of one or two kinds. Bordered pits on the tangential walls of the summer wood either numerous (Sec. I) or usually wanting (Sec. II). Tracheids wholly without spirals. Resinous tracheids sometimes present, the resin forming radial plates opposite the rays and simulating Sanio's bands.

*Tangential.* Fusiform rays chiefly large and broad; the cells of the inflated portion chiefly large and thin-walled; the central tract occupied by 1 large resin passage with thyloses and thin-walled epithelium. Ordinary rays chiefly 1-seriate, more or less conspicuously contracted by the interspersed tracheids.

## SYNOPSIS OF SPECIES

### A. PINUS PROPER

#### *Existing Species*

*Sec. I. Pits on the tangential walls of the summer wood prominent. Medullary tracheids prominent, sparingly interspersed, their upper and lower walls not dentate.*

A. The lateral walls of the ray cells (radial) with small, numerous, and more or less conspicuously bordered pits; the upper and lower walls thick and coarsely pitted; the terminal walls coarsely pitted; the thick side walls (tangential) not inflated or incurved. The rays sometimes show thin-walled cells without pits, which are conterminous and interspersed.

Ray cells (radial) of 1 kind only, all thick-walled and strongly pitted.

Rays nonresinous (radial), the tracheids numerous, marginal, often interspersed.

Pits on the lateral walls of the ray cells 1-4, chiefly 4, throughout, but finally 2, per tracheid in the outer summer wood.

Ray cells (tangential) conspicuously unequal and variable, from round to oval or oblong, those of the low rays often three times higher than wide.

#### 3. *P. monophylla.*

Rays more or less resinous (radial), the tracheids marginal, sparingly or rarely interspersed.

Pits on the lateral walls of the ray cells 2-4 per tracheid throughout.

Ordinary rays (tangential) sparingly resinous, somewhat contracted by occasionally interspersed, narrowly oval, or oblong tracheids; the cells equal and chiefly uniform, oval to oblong, rarely narrow.

#### 1. *P. Parryana.*

Ordinary rays (tangential) somewhat resinous, rather broad, not perceptibly contracted by the occasionally interspersed

and equal tracheids ; the cells very equal, chiefly very uniform, narrowly oval or oblong, rarely broader.

2. *P. cembroides*.

Pits on the lateral walls of the ray cells 1-5 throughout, or finally 1-2, per tracheid in the summer wood.

Ordinary rays rather broad and nonresinous (tangential), somewhat contracted by the narrower and smaller, occasionally interspersed tracheids ; the cells very equal and uniform, narrowly oval to oblong.

4. *P. Balfouriana*.

Ray cells (radial) of 2 kinds: (1) thick-walled and strongly pitted; (2) thin-walled, devoid of pits, conterminous, and interspersed.

Pits on the lateral walls of the ray cells 3-6, soon 4, or in the outer summer wood 2, per tracheid.

Ordinary rays (tangential) nonresinous, numerous, the cells equal, uniform, oval, or oblong.

Fusiform rays (tangential) few, narrow.

5. *P. aristata*.

Pits on the lateral walls of the ray cells 1-4 throughout, or in the marginal cells upwards of 5 or 6, per tracheid.

Ordinary rays (tangential) numerous, broad, the cells chiefly equal, uniform, oval, and narrow.

Fusiform rays (tangential) rather numerous, small, and narrow.

6. *P. edulis*.

*B.* Lateral walls of the ray cells (radial) with large, open, and simple, oval, or lenticular pits, 1-2 per tracheid ; the upper and lower walls thin and distantly or even obscurely pitted; the terminal walls thin and entire or locally thickened ; the thin side walls (tangential) either inflated or incurved.

Ray cells (transverse or tangential) with their very thin side walls strongly inflated and projecting into the cavities of the adjacent tracheids.

Pits on the lateral walls of the ray cells oval or squarish, or finally lenticular, 1-2, chiefly 1, per tracheid throughout.

Resin passages numerous and large, chiefly in or near the summer wood ; when in the former situation, central to a large tract of thin-walled tracheids.

10. *P. reflexa*.

Ray cells (transverse or tangential) with their thin side walls not strongly inflated, but commonly incurved or sometimes convex.

Pits on the lateral walls of the ray cells chiefly 1-2 per tracheid.

Resinous tracheids (radial) not present.

Rays (tangential) strongly resinous, the cells oval, unequal, variable.

Pits on the lateral walls of the ray cells 1-2, in the summer wood reduced to 1, per tracheid.

8. *P. monticola*.

Rays (tangential) nonresinous.

Ray cells (tangential) oval, equal, and uniform.

Pits on the lateral walls of the ray cells 1-2, or in the marginal cells 3-4, per tracheid.

9. *P. flexilis*.

Ray cells (tangential), oblong, narrow, equal, and uniform.

Pits on the lateral walls of the ray cells 1-2 throughout, rarely 3, per tracheid.

11. \* *P. strobus*.

Ray cells (tangential) chiefly equal, but more or less variable, from broadly to narrowly oval or oblong.

Pits on the lateral walls of the ray cells 2 per tracheid throughout, rarely 1 or 3.

7. *P. Lambertiana*.

Ray cells (tangential) oblong and narrow, more rarely oval and broader, not very variable.

Pits on the lateral walls of the ray cells 1 per tracheid throughout, or in the early spring wood 2 per tracheid.

12. *P. parviflora*.

Resinous tracheids (radial or tangential) present, the resin in plates opposite the rays and simulating Sanio's bands.

Rays (tangential) nonresinous.

Ray cells (tangential) oval or oblong, not very variable.

Pits on the lateral walls of the ray cells 1 per tracheid throughout, more rarely 2.

13. *P. albicaulis*.

Ray cells (tangential) oblong and narrow, more rarely oval and broader, not very variable.

Pits on the lateral walls of the ray cells 1 per tracheid throughout, or in the early spring wood 2 per tracheid.

12. *P. parviflora*.

*Sec. II. Pits on the tangential walls of the summer wood usually wanting. Medullary tracheids prominent, more or less, often strongly, interspersed, their upper and lower walls dentate or the teeth so prolonged and united across the cavity as to form a more or less definite and sometimes very strongly defined reticulum.*

A. Pits on the lateral walls of the ray cells large and open, chiefly 1, and not exceeding 2, per tracheid.

Ray cells of 1 kind only.

Pits on the lateral walls of the ray cells simple throughout.

Epithelium of the resin passages resinous.

Bordered pits in 1 row, sometimes in pairs.

Ray tracheids simply dentate, rarely interspersed.

Pits on the lateral walls of the ray cells 1-2, chiefly 1, per tracheid.

21. *P. resinosa*.

Ray tracheids simply dentate, but numerous and interspersed and often predominant.

Pits on the lateral walls of the ray cells large, oval, oblong, or lenticular, 1-2, chiefly 1, per tracheid.

22. *P. tropicalis*.

Pits on the lateral walls of the ray cells large and conspicuously bordered in the summer wood.

Epithelium of the resin passages nonresinous.

Resin passages (transverse) large, numerous, scattering.

Bordered pits in 1 row.

Ray tracheids (radial or tangential) simply dentate, not interspersed.

Pits on the lateral walls of the ray cells 1, rarely 2, per tracheid.

23. *P. Thunbergii*.

Ray tracheids (radial or tangential) somewhat interspersed, sparingly reticulated in the summer wood.

Pits on the lateral walls of the ray cells strictly 1 per tracheid.

24. *P. densiflora*.

B. Pits on the lateral walls of the ray cells generally rather small and upwards of 6 per tracheid, at least 2 or more per tracheid.

Ray cells (radial) of 1 kind only and thin-walled.

Fusiform rays (tangential) with the cells of the inflated portion *all* or chiefly rather thick-walled.

Epithelium of the resin passages (transverse) chiefly in 1-2 rows, resinous.

Summer wood dense.

Bordered pits in 1 row, or sometimes in pairs.

Pits on the lateral walls of the ray cells 1-6 per tracheid.

Ray tracheids strongly predominant and strongly reticulated throughout.

17. *P. Banksiana*.

Fusiform rays (tangential) with the cells of the inflated portion *all* or chiefly thin-walled, all broken out.

Epithelium of the resin passages (transverse) chiefly or wholly in 1 row, nonresinous (rarely resinous in *P. tæda* and *P. rigida*).

Summer wood open.

Bordered pits in 1 row, sometimes in pairs.

Pits on the lateral walls of the ray cells 1-5, chiefly 2, per tracheid, becoming bordered in the summer wood.

Ray tracheids sparingly interspersed, strongly reticulated throughout.

15. *P. rigida*.

Pits on the lateral walls of the ray cells 1-4, rarely 5, per tracheid.

Ray tracheids more or less reticulated in the summer wood, often interspersed.

25. *P. Murrayana*.

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids sparingly (very rarely strongly) reticulated throughout.

39. *P. tæda*, Linn.

Pits on the lateral walls of the ray cells 1-5 per tracheid.

Ray tracheids when interspersed very low, strongly reticulated throughout.

14. *P. clausa*.

Summer wood dense.

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids sparingly (rarely strongly) reticulated throughout.

39. *P. tæda*.

Ray tracheids high, very strongly reticulated throughout.

The ray cells apparently all of 1 kind, but differentiating slightly.

41. *P. cubensis*.

Pits on the lateral walls of the ray cells 1-5 per tracheid.

Ray tracheids strongly reticulated throughout, often predominant, and, when interspersed, very low.

14. *P. clausa*.

Pits on the lateral walls of the ray cells 1-4 per tracheid.

Ray tracheids chiefly high, conspicuously predominant, and strongly reticulated throughout.

20. *P. echinata*.

Bordered pits in 1 row, sometimes in pairs.

Pits on the lateral walls of the ray cells 1-4 per tracheid.

Ray tracheids chiefly high, conspicuously predominant, and strongly reticulated throughout.

20. *P. echinata*.

Epithelium of the resin passages (transverse) distinctly in 1 or more rows, nonresinous.

Summer wood dense, rarely somewhat open.

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids sparingly (rarely strongly) reticulated throughout.

39. *P. tæda*.

Ray tracheids high, very strongly reticulated throughout.

Ray cells apparently all of 1 kind, but differentiating slightly.

41. *P. cubensis*.

Pits on the lateral walls of the ray cells 2-5, chiefly 4, per tracheid.

Ray tracheids commonly predominant and interspersed, very strongly reticulated throughout.

40. *P. palustris*.

Epithelium of the resin passages (transverse) distinctly in 1 or more rows, resinous.

Summer wood open.

Bordered pits in 1 row or sometimes in pairs.

Pits on the lateral walls of the ray cells 1-4, rarely 5, per tracheid.

Ray tracheids sparingly interspersed, strongly reticulated throughout.

16. *P. serotina*.

Pits on the lateral walls of the ray cells 1-5, chiefly 2, per tracheid, becoming bordered in the summer wood.

Ray tracheids sparingly interspersed, strongly reticulated throughout.

15. *P. rigida*.

Bordered pits in 1 row.

Pits on the lateral walls of the ray cells 1-6, chiefly 2 or 3, per tracheid, but very variable.

Ray tracheids often predominant, interspersed, sparingly reticulated.

19. *P. glabra*.

Summer wood dense (sometimes open in *P. tæda* and *P. cubensis*).

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids sparingly (very rarely strongly) reticulated throughout.

39. *P. tæda*.

Ray tracheids high, very strongly reticulated throughout.

Ray cells apparently all of one kind, but differentiating slightly.

41. *P. cubensis*.

Pits on the lateral walls of the ray cells 2-5, chiefly 4, per tracheid.

Ray tracheids commonly predominant and interspersed, very strongly reticulated throughout.

40. *P. palustris*.

Bordered pits in 1 row.

Pits on the lateral walls of the ray cells 1-6, chiefly 2 or 3, per tracheid, but very variable.

Ray tracheids interspersed, often predominant, sparingly reticulated.

19. *P. glabra*.

Bordered pits in 1 row, or sometimes in pairs.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids high, very strongly reticulated throughout.

Ray cells apparently all of one kind, but differentiating slightly.

41. *P. cubensis*.

Pits on the lateral walls of the ray cells 1-6 per tracheid.

Ray tracheids strongly predominant and strongly reticulated throughout.

17. *P. Banksiana*.

Pits on the lateral walls of the ray cells 1-4, rarely 5, per tracheid.

Ray tracheids sparingly interspersed, strongly reticulated throughout.

16. *P. serotina*.

Pits on the lateral walls of the ray cells 1-5, chiefly 2, per tracheid, becoming bordered in the summer wood.

Ray tracheids sparingly interspersed, strongly reticulated throughout.

15. *P. rigida*.

Pits on the lateral walls of the ray cells 1-4, chiefly 2, per tracheid.

Ray tracheids sparingly interspersed, distinctly reticulated throughout.

18. *P. contorta*.

Ray cells (radial) of 2 kinds: (1) thick-walled; and (2) thin-walled.

Fusiform rays (tangential) with the cells of the inflated portion *all* or chiefly thick-walled.

Epithelium of the resin passages (transverse) in 1-2 or more rows, nonresinous.

Summer wood dense.

Bordered pits in 1 row or sometimes in pairs.

Pits on the lateral walls of the ray cells (1) 1-3, bordered in the summer wood; and (2) 1-4, chiefly 2-3, per tracheid.

Ray tracheids more or less interspersed, reticulated throughout.

34. *P. pungens*.

Epithelium of the resin passages (transverse) in 1-2 or more rows, resinous.

Summer wood open.



Bordered pits in 1 row or sometimes in pairs.

Pits on the lateral walls of the ray cells 1-5, chiefly 2, per tracheid, becoming bordered in the summer wood.

Ray tracheids sparingly interspersed, strongly reticulated throughout.

15. *P. rigida*.

Pits on the lateral walls of the ray cells (1) 1-4; and (2) 1-3, chiefly 2, per tracheid, the two forms of cells clearly defined.

Ray tracheids reticulated in the summer wood, predominant in the low rays of which they often compose the entire structure.

36. *P. muricata*.

Pits on the lateral walls of the ray cells 2-4 throughout, the two forms of cells merging and not always clearly defined.

Ray tracheids strongly dentate and becoming sparingly reticulated in the summer wood, interspersed, often predominant.

30. *P. chihuahuana*.

Summer wood dense.

Bordered pits in 1 row or sometimes in pairs.

Pits on the lateral walls of the ray cells 2-4 throughout, the two forms of cells merging and not always clearly differentiated.

Ray tracheids strongly dentate and becoming sparingly reticulated in the summer wood, interspersed, often predominant.

30. *P. chihuahuana*.

Fusiform rays (tangential) with the cells of the inflated portion all thin-walled and usually broken out.

Epithelium of the resin passages (transverse) in 1-2 or more rows, nonresinous.

Summer wood open.

Bordered pits in 1 row.

Pits on the lateral walls of the ray cells 1-6, chiefly 2 or 3, per tracheid, but very variable.

Ray tracheids interspersed, often predominant, sparingly reticulated.

19. *P. glabra*.

Pits on the lateral walls of the ray cells (1) 1-4; and (2) 2-4, chiefly 4, per tracheid.

Ray tracheids predominant, sparingly reticulated.

33. *P. scopulorum*.

Bordered pits in 1 row, sometimes in pairs.

Pits on the lateral walls of the ray cells 1-4, rarely 5, per tracheid.

Ray tracheids more or less reticulated in the summer wood, often interspersed.

25. *P. Murrayana*.

Pits on the lateral walls of the ray cells 2-5, chiefly 3-4, per tracheid.

Ray tracheids strongly predominant, strongly dentate, and more or less reticulated throughout.

31. *P. Jeffreyi*.

Pits on the lateral walls of the ray cells (1) 1-4; and (2) 1-3, chiefly 2, per tracheid.

Ray tracheids often predominant, reticulated throughout.

27. *P. Coulteri*.

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids sparingly (rarely strongly) reticulated throughout.

39. *P. tæda*.

Ray tracheids high, very strongly reticulated throughout.

41. *P. cubensis*.

Summer wood dense, more rarely somewhat open.

Bordered pits in 1 row.

Pits on the lateral walls of the ray cells (1) 1-4; and (2) 2-4, chiefly 4, per tracheid.

Ray tracheids predominant, sparingly reticulated.

33. *P. scopulorum*.

Bordered pits in 1 row, sometimes in pairs.

Pits on the lateral walls of the ray cells (1) 1-4; and (2) 1-3, chiefly 2, per tracheid, the two forms of cells clearly defined.

Ray tracheids reticulated in the summer wood, predominant in the low rays of which they often compose the entire structure.

36. *P. muricata*.

Pits on the lateral walls of the ray cells (1) 1-3, bordered in the summer wood; and (2) 1-4, chiefly 2-3, per tracheid.

Ray tracheids more or less interspersed, reticulated throughout.

34. *P. pungens*.

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 2-5, chiefly 4, per tracheid.

Ray tracheids commonly predominant and interspersed, very strongly reticulated throughout.

40. *P. palustris*.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids high, very strongly reticulated throughout.

41. *P. cubensis*.

Epithelium of the resin passages (transverse) in 1-2 or more rows, resinous.

Summer wood dense.

Bordered pits in 1 row.

Pits on the lateral walls of the ray cells 1-6, chiefly 2 or 3, per tracheid, but very variable.

Ray tracheids interspersed, often predominant, sparingly reticulated.

19. *P. glabra*.

Pits on the lateral walls of the ray cells 2-4 per tracheid, rarely 5.

Ray tracheids strongly reticulated, often predominant.

32. *P. ponderosa*.

Bordered pits in 1 row, sometimes in pairs.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids sparingly (rarely strongly) reticulated throughout.

39. *P. tæda*.

Pits on the lateral walls of the ray cells (1) 2-6, chiefly 4; and (2) 1-4, chiefly 4, per tracheid.

Ray tracheids predominant, very strongly reticulated throughout.

35. *P. inops*.

Bordered pits in 1-2 rows.

Pits on the lateral walls of the ray cells 1-6, chiefly 2-4, per tracheid.

Ray tracheids high, very strongly reticulated throughout.

41. *P. cubensis*.

Pits on the lateral walls of the ray cells 2-5, chiefly 4, per tracheid.

Ray tracheids sparingly interspersed, predominant, strongly dentate, and somewhat reticulated in the summer wood.

38. *P. Sabiniana*.

Ray tracheids commonly predominant, often interspersed and very strongly reticulated throughout.

40. *P. palustris*.

Pits on the lateral walls of the ray cells 1-6, chiefly 4, per tracheid.

Ray tracheids sparingly (rarely strongly) reticulated throughout.

39. *P. tæda*.

Summer wood open.

Bordered pits in 1 row or sometimes in pairs, the latter sometimes numerous (*P. arizonica*).

Pits on the lateral walls of the ray cells (1) 1-2, rarely 6, chiefly 2; and (2) 1-3 per tracheid.

Tracheids sparingly predominant and sparingly reticulated.

37. *P. insignis*.

Pits on the lateral walls of the ray cells (1) 2-4; and (2) 2-3 per tracheid.

Ray tracheids strongly predominant and strongly reticulated.

29. *P. Torreyana*.

Pits on the lateral walls of the ray cells 2-4 per tracheid.

Ray tracheids dentate and somewhat reticulated throughout, sometimes interspersed and predominant.

28. *P. tuberculata*.

Pits on the lateral walls of the ray cells 2-4, chiefly 4, per tracheid.

Ray tracheids strongly predominant, strongly dentate, and somewhat reticulated in the summer wood.

26. *P. arizonica*.

Pits on the lateral walls of the ray cells (1) 1-6, chiefly 4; and (2) 1-4, chiefly 4, per tracheid.

Ray tracheids predominant, very strongly reticulated throughout.

35. *P. inops*.

Bordered pits in 1 row.

Pits on the lateral walls of the ray cells 1-6, chiefly 2 or 3, per tracheid, but very variable.

Ray tracheids often predominant, interspersed, sparingly reticulated.

19. *P. glabra*.

## B. \*\* PITYOXYLON (Pinoxylon)

### *Extinct Species*

Ray tracheids present.

Upper and lower walls of the ray tracheids dentate.

Bordered pits in 2 rows.

Resin passages numerous, large, scattering.

Pits on the lateral walls of the ray cells 1-2 per tracheid.

42. \*\* *P. (Pinoxylon) dacotense*.

Upper and lower walls of the ray tracheids not dentate.

Bordered pits in 1 row.

Transition from the spring to the summer wood gradual.

Ordinary rays (tangential) 1-2 seriate in part.

Resin passages (transverse) very large.

Medullary rays (transverse) distant 3-8, more rarely 8, rows of tracheids.

43. \*\* *P. Aldersoni*.

Ordinary rays (tangential) strictly 1-seriate.

Resin passages (transverse) very large.

Medullary rays (transverse) distant upwards of 25 rows of tracheids.

44. \*\* *P. amethystinum*.

Resin passages (transverse) rather large, the epithelial cells resinous.

Medullary rays (transverse) distant upwards of 9, or rarely 15, rows of tracheids.

45. \*\* *P. (Pinus) columbiana*.

Resin passages obliterated.

Bordered pits on the lateral walls of the ray cells 2-3 per tracheid.

46. \*\* *P. Peali*.

Bordered pits in 1-3, chiefly 2, rows, round or hexagonal.

Ordinary rays (tangential) 2-seriate in part.

Resin passages not represented.

47. \*\* *P. chasense*.

Ray tracheids wholly wanting.

Bordered pits in 1 row.

Resin passages numerous, large, chiefly in the summer wood, filled with prominent and resinous thyloses, the epithelium 1-2 cells thick, not extended into parenchymatous tracts.

48. \*\* *P. statenense*.

Resin passages numerous, small, chiefly in the summer wood, devoid of thyloses, the epithelium composed of a single layer which extends into a prominent and often broad tract of wood parenchyma.

49. \*\* *P. scituate*.

## A. PINUS PROPER

### *Existing Species*

### *Section I. Soft Pines*

#### 1. *P. Parryana*, Engelm.

##### *Pinon. Nut Pine*

*Transverse.* Growth rings chiefly narrow but very variable. Summer wood very open and chiefly very thin, but in the broader rings upwards of one half the spring wood, from which the transition is very gradual; the tracheids in regular rows, conspicuously unequal and rounded. Spring tracheids squarish-hexagonal, unequal in regular rows, the walls rather thin. Medullary rays numerous, broad, 1 cell wide, distant 2-6 rows of tracheids. Resin passages numerous, medium, and variable, very scattering throughout the entire growth ring; the several-layered epithelium composed of very large, rather thick-walled cells, more or less resinous.

*Radial.* Rays sparingly resinous; the tracheids numerous, marginal, high, rarely interspersed. Parenchyma ray cells chiefly straight and rather narrow, but in the narrower growth rings and in the summer wood becoming shorter and distinctly fusiform; the upper and lower walls thick and conspicuously though often distantly pitted, becoming more strongly pitted in the fusiform cells; the terminal walls locally thickened or coarsely pitted; the lateral walls with small, round pits with a more or less definite though variable border and a lenticular orifice, 2-4 per tracheid. Bordered pits in 1 row, rather numerous, broadly

elliptical. Pits on the tangential walls of the summer wood rather numerous, small and chiefly confined to the two outermost walls. Resinous tracheids wanting.

*Tangential.* Fusiform rays numerous, very narrow; the cells of the inflated portion all thin-walled and usually much broken out; the somewhat thicker-walled structure of the central tract generally present and embracing a small resin canal. Ordinary rays sparingly resinous, medium, numerous, broad, somewhat contracted by occasionally interspersed, narrowly oval or oblong tracheids; the thick-walled cells usually equal and somewhat uniform, oval to oblong, rarely narrow. Resinous tracheids wanting.

A small tree 6-9 m. high, with a trunk upwards of .45 m. in diameter. Wood light, soft, close grained, and compact.

Relative specific gravity . . . . .	0.5675
Percentage of ash residue . . . . .	0.54
Approximate relative fuel value . . . . .	56.44
Coefficient of elasticity in kilograms on millimeters . . . . .	378.
Ultimate transverse strength in kilograms . . . . .	182.
Ultimate resistance to crushing in kilograms . . . . .	5420.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	3126.
(Sargent)	

Larkin's Station, San Diego County, California, and southward into Lower California, where it forms extensive forests on high mesas and slopes (Sargent).

## 2. *P. cembroides*, Zucc.

### *Pinon. Nut Pine*

*Transverse.* Growth rings not broad, variable, more or less conspicuously double, the structure as a whole rather dense. Summer wood rather open, either very thin or upwards of equal to the spring wood, from which the transition is very gradual and from which it cannot be readily distinguished; the tracheids distinctly rounded, unequal, but in rather regular rows. Spring tracheids hexagonal, not large, very unequal and variable, but in regular rows. Medullary rays prominent and numerous, broad, 1 cell wide, distant 1-6, rarely 10, rows of tracheids. Resin passages numerous, not large, chiefly in the middle or inner portion of the growth ring, the several-layered epithelium composed of large, thick- and thin-walled, nonresinous cells.

*Radial.* Rays somewhat resinous, the resin localized, granular, rarely massive; the tracheids not very numerous, marginal, rarely interspersed; the lateral walls with very small pits about 2 per tracheid. Parenchyma ray cells conspicuously contracted at the ends throughout, short, equal to 8-10 tracheids; the upper and lower walls thick, uniform, conspicuously pitted throughout; the terminal walls thin but locally thickened or more often coarsely pitted; the lateral walls with small, round pits, with a more or less obvious though very unequal border and a lenticular orifice, at first 2-4, but in the summer wood

reduced to 2, and finally to 1, per tracheid, when they take the form of very narrow and much prolonged slits. Bordered pits in 1 row, numerous. Pits on the tangential walls of the summer wood small and numerous, extending far into the summer wood. Resinous tracheids wanting.

*Tangential.* Fusiform rays numerous, very narrow, usually high, the cells of the inflated portion very thin-walled and chiefly wanting, except the persistent, thicker-walled central tract, which includes a small resin canal. Ordinary rays numerous, medium, somewhat resinous, rather broad, not perceptibly contracted by the occasionally interspersed, equal, but higher and oblong tracheids; the cells thick-walled, very equal, chiefly very uniform, and narrowly oval or oblong, rarely broader. Resinous tracheids wanting.

A small tree 6-7 m. high, with a trunk rarely exceeding .30 m. in diameter. Wood light, soft, very close grained, and compact.

Specific gravity . . . . .	0.6512
Percentage of ash residue . . . . .	0.90
(Sargent)	

Dry ridges and slopes at 3500 feet elevation. Santa Catalina Mountains of Arizona and through northern Mexico (Sargent).

### 3. *P. monophylla*, Torr.

#### *Pinon. Nut Pine*

*Transverse.* Growth rings thin, unequal, often double. Summer wood thin, of 3-5 tracheids and open, the tracheids in more or less irregular rows, unequal. Spring tracheids squarish-hexagonal, rather variable, not large, the walls rather thin and commonly showing the secondary wall infolded. Medullary rays not very prominent, numerous, broad, 1 cell wide, distant 1-6, or more rarely 10, rows of tracheids. Resin passages very large and numerous, the several-layered epithelium composed of large and variable cells, both thick- and thin-walled.

*Radial.* Rays nonresinous; the tracheids numerous, marginal, often interspersed. Parenchyma ray cells short, strongly contracted at the ends; the terminal walls commonly thick and coarsely pitted; the upper and lower walls thick and strongly pitted; the lateral walls with more or less obviously-bordered pits, with a prolonged, slit-like orifice which becomes lenticular in the earlier spring wood, 1-4, chiefly 4, per tracheid, finally reduced to 2 in the outer summer wood. Bordered pits numerous, in 1 row, elliptical. Pits on the tangential walls of the summer wood numerous, medium to large, conspicuously lenticular. Resinous tracheids wanting.

*Tangential.* Fusiform rays rather numerous and narrow, the cells of the inflated portion large and very thin-walled, often much broken out, the persistent central tract containing a resin canal of medium size. Ordinary rays numerous, broad, very sparingly resinous, not contracted by interspersed tracheids; the cells conspicuously unequal and variable,



from round to oval or oblong, those of the low rays often three times higher than wide, those of the higher rays sometimes twice the width of others.

A small, bushy tree 4-6 m. high, with a trunk upwards of 1 m. in diameter. Wood light, soft, weak, brittle, close grained, and compact.

Specific gravity . . . . .	0.5658
Percentage of ash residue . . . . .	0.68
Approximate relative fuel value . . . . .	56.20
Coefficient of elasticity in kilograms on millimeters . . . . .	435.
Ultimate transverse strength in kilograms . . . . .	123.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4389.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2713.
(Sargent)	

Dry gravelly slopes and mesas between 3000 and 6000 feet elevation. Near Lake Utah, to the eastern foothills of the California Sierras, and south along the mountain ranges of the Great Basin to the San Francisco Mountains of eastern Arizona (Sargent).

#### 4. *P. Balfouriana*, A. Murr.

##### *Foxtail Pine*

*Transverse.* Growth rings narrow, uniform, the structure very open throughout. Summer wood thin, of 2-6 tracheids and open, the tracheids large in regular rows, uniform, the transition from the spring wood gradual. Spring tracheids rather large, very thin-walled, hexagonal, chiefly in regular rows, but conspicuously unequal. Medullary rays rather prominent and numerous, broad, 1 cell wide, distant 2-8 rows of tracheids. Resin passages medium, rather numerous, widely scattering, the somewhat extensive epithelium composed of large, thin-walled, more or less resinous cells.

*Radial.* Rays sparingly resinous; the tracheids rather numerous, marginal, rarely interspersed. Parenchyma ray cells short and straight; the upper and lower walls thick and very strongly pitted; the lateral walls with numerous, small, round, or oval pits, at first with a prominent border and narrowly lenticular, prolonged orifice, the border becoming obscure and variable toward the summer wood, and the orifice broader, 1-5 per tracheid, finally reduced to 1-2 in the summer wood. Bordered pits numerous and round, in 1 row, nearly as broad as the tracheid. Pits on the tangential walls of the summer wood very numerous and contiguous on the outermost wall, becoming scattering in the older tracheids, small but rather broadly lenticular. Resinous tracheids wanting.

*Tangential.* Fusiform rays narrow, the cells of the inflated portion large, thin-walled, resinous, the resin passage not large. Ordinary rays medium to high, rather broad, nonresinous, and somewhat contracted by the rather narrower, smaller, and occasionally interspersed tracheids; the thick-walled cells very equal and uniform, narrowly oval to oblong.

A small tree 15–19 m. high, with a trunk upwards of .90 m. in diameter. Wood light, soft, weak, brittle, very close grained, compact, satiny, and susceptible of a good polish.

Specific gravity . . . . .	0.5434
Percentage of ash residue . . . . .	0.41
Approximate relative fuel value . . . . .	54.17
Coefficient of elasticity in kilograms on millimeters . . . . .	594.
Ultimate transverse strength in kilograms . . . . .	181.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5398.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2350.
(Sargent)	

Dry, open ridges, forming upon Scott's Mountain a broad belt of open forest between 5000 and 8000 feet elevation. Mt. Whitney, California, and about the head waters of the King and Kern rivers (Sargent).

### 5. *P. aristata*, Engelm.

*Foxtail Pine. Hickory Pine*

**Transverse.** Summer wood thin, upwards of 8 tracheids, barely distinguishable, very open, the tracheids often variable in more or less conspicuously irregular rows. Spring tracheids rather large, conspicuously squarish-hexagonal, very uniform in regular rows, the walls thin, the transition to the summer wood very gradual. Medullary rays rather prominent and broad, 1 cell wide, distant 2–6, more rarely 10, rows of tracheids. Resin passages numerous, rather large, the rather extensive and many-layered epithelium composed of large, very thin-walled, nonresinous cells.

**Radial.** Rays sparingly resinous throughout; the tracheids numerous, marginal, sparingly interspersed. Parenchyma ray cells of 2 kinds: (1) the cells more or less strongly contracted at the ends; the upper and lower walls thick, strongly pitted; the terminal walls coarsely pitted; the lateral walls with round or oval but rather small pits, with a lenticular orifice and an obvious border which becomes variable and obscure toward the summer wood, at first 3–6, soon uniformly about 4, or in the outermost summer wood 2, per tracheid; and (2) cells occasionally interspersed and often conterminous with the cells of the first kind; the terminal walls thin and not pitted, but often locally thickened; the upper and lower walls thin and not pitted; the lateral walls devoid of pits. Bordered pits numerous, in 1 row, elliptical, as broad as the tracheid. Pits on the tangential walls of the summer wood chiefly confined to the outermost wall, where they are numerous, apparently not extending beyond the second wall, small, distinctly lenticular. Resinous tracheids wanting.

**Tangential.** Fusiform rays rather few, narrow, the cells of the short terminals thick-walled, those of the inflated portion very thin-walled and much broken down or wanting, the more persistent central tract with a rather small resin passage with delicate epithelium. Ordinary rays

numerous, nonresinous, low to medium, slightly contracted by the occasionally interspersed tracheids. Parenchyma ray cells not very thick-walled, equal, rather uniform and oval, more rarely becoming either round, oval, or oblong; sometimes with interspersed thin-walled cells of similar form and size.

A tree 15-30 m. high, with a trunk upwards of 2.40 m. in diameter.

Wood light, soft, not strong, very close grained, and compact.

Specific gravity . . . . .	0.5572
Percentage of ash residue . . . . .	0.30
Approximate relative fuel value . . . . .	55.56
Coefficient of elasticity in kilograms on millimeters . . . . .	715.
Ultimate transverse strength in kilograms . . . . .	279.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5209.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2140.
(Sargent)	

Dry, gravelly ridges; mountains of southeastern California, Nevada, northern Arizona, and southern Utah to Colorado above 7500 feet, in Colorado reaching 12,000 feet (Sargent).

#### 6. *P. edulis*, Engelm.

*Pinon. Nut Pine*

*Transverse.* Growth rings narrow, unequal. Summer wood thin, of 3-4 tracheids, and not prominent, but very open throughout; the tracheids strongly unequal in conspicuously irregular rows, the walls thin, the transition to the spring wood gradual. Spring tracheids open, squarish, unequal, and in more or less irregular rows, the walls thin. Medullary rays not very prominent, numerous, rather broad, 1 cell wide, distant 2-7 rows of tracheids. Resin passages numerous, large, the many-layered epithelium often forming extensive tracts composed of large and very variable, often thick-walled, somewhat resinous cells.

*Radial.* Rays very sparingly resinous; the tracheids marginal, rarely interspersed. Parenchyma ray cells conspicuously narrower at the ends, short, of 2 kinds: (1) the upper and lower walls thick and entire or distantly pitted, becoming more strongly pitted locally or in the summer wood; the terminal walls generally thick and coarsely pitted or rarely thin and devoid of pits; the lateral walls with small and round pits with a variable, often obscure border and a lenticular orifice, 1-4, more rarely 5 or 6, in the marginal cells, in the summer wood becoming 2, per tracheid; and (2) thin-walled cells sparingly interspersed and conterminous with those of the first kind; the terminal walls thin and locally thickened; the upper and lower as well as the lateral walls devoid of pits. Bordered pits numerous, small, elliptical, in 1 row. Pits on the tangential walls of the summer tracheids numerous on the outermost wall, becoming fewer in the older tracheids, rather small and broadly lenticular. Resinous tracheids wanting.

*Tangential.* Fusiform rays rather numerous, chiefly small and narrow; the inflated portion with rather large and very thin-walled cells; the resin passage small. Ordinary rays low to medium, numerous, rather broad, not restricted by the equal and occasionally interspersed tracheids; the cells chiefly equal, rather uniform, oval, chiefly narrow and thick-walled, but sometimes with interspersed thin-walled cells often of greater height.

A small tree 6–9 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, soft, not strong, brittle, close grained, compact, and durable in contact with the soil.

Specific gravity . . . . .	0.6388
Percentage of ash residue . . . . .	0.62
Approximate relative fuel value . . . . .	63.49
Coefficient of elasticity in kilograms on millimeters . . . . .	421.
Ultimate transverse strength in kilograms . . . . .	191.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5578.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	3388.

(Sargent)

Eastern base of Pikes Peak, Colorado; south through New Mexico to the mountains of western Texas. Dry mesas and slopes, generally on lime or sandstone, reaching elevations of 9000 feet in Colorado (Sargent).

## 7. *P. Lambertiana*, Douglas

### *Sugar Pine*

*Transverse.* Growth rings narrow, uniform. Summer wood about one fourth to one third the spring wood, from which the transition is gradual, the structure rather open. Spring tracheids large, squarish-hexagonal, in regular rows, very uniform, the walls thin. Medullary rays not very prominent or numerous, rather broad, 1 cell wide, distant 2–18 rows of tracheids. Resin passages very large, rather numerous, the epithelium prominent, of several layers composed of very thin-walled cells, very resinous.

*Radial.* Rays barely if at all resinous; the tracheids short, rather broad, marginal and sparingly interspersed and then very narrow. Parenchyma ray cells chiefly straight; the upper and lower walls thin and obscurely pitted; the terminal walls thin and not pitted but sometimes locally thickened; the lateral walls with very large, oval pits, chiefly 2 per tracheid throughout, rarely 1 or 3. Bordered pits distinctly in 1–2 rows, elliptical, numerous. Pits on the tangential walls of the summer wood numerous, but rather small and narrowly lenticular, not confined to the outermost walls. Resinous tracheids wanting.

*Tangential.* Fusiform rays numerous, large, and very broad, the inflated portion composed of rather thin-walled, often strongly resinous, cells, the very large resin passage with thin-walled epithelium. Ordinary rays rather numerous, nonresinous, low to medium, strongly constricted at

the position of the very narrow and small, interspersed tracheids ; the parenchyma cells rather equal but variable from broadly to narrowly oval, the thin side walls sometimes strongly inflated, rarely incurved.

A large tree 46-92 m. high, with a trunk upwards of 7 m. in diameter.

Wood very light, soft, coarse, but straight grained, compact, satiny, and easily worked.

Specific gravity . . . . .	0.3684
Percentage of ash residue . . . . .	0.22
Approximate relative fuel value . . . . .	36.76
Coefficient of elasticity in kilograms on millimeters . . . .	794.
Ultimate transverse strength in kilograms . . . . .	255.
Ultimate resistance to longitudinal crushing in kilograms . .	5382.
Resistance to indentation to 1.27 mm. in kilograms . . . .	1244.

(Sargent)

Cascade and Coast Ranges of Oregon, where it descends to 1000 feet above sea level, from the head of the Mackenzie River and the valley of the Rogue, southward along the western flanks of the California Sierras, where it reaches an elevation of 4000-8000 feet; through the coast ranges to the Santa Lucia Mountains, and in the San Bernardino and Cuyamaca mountains (Sargent).

### 8. *P. monticola*, D. Don

#### *White Pine*

*Transverse.* Growth rings variable. Summer wood open and *very thin* and imperceptibly passing into the spring wood, the tracheids in regular rows, variable, squarish. Spring wood very open, the tracheids large and squarish, rather thin-walled. Medullary rays prominent and resinous, not numerous, rather broad, 1 cell wide, distant 2-17 rows of tracheids. Resin passages very large, rather numerous, the epithelium rather extensive and resinous.

*Radial.* Rays conspicuously resinous throughout, the ray tracheids narrow, marginal, often interspersed. Parenchyma ray cells straight; the upper and lower walls thin and entire or again with locally numerous, broad pits, unequal; the terminal walls thin and entire or again locally thickened; the lateral walls with very large, oval or oblong or lenticular pits, chiefly 1-2 per tracheid throughout, in the summer wood reduced to 1 with a lenticular orifice. Bordered pits round or elliptical, in 1 row or sometimes in pairs. Pits on the tangential walls of the summer wood small and narrowly lenticular, chiefly on the outermost wall. Resinous tracheids wanting.

*Tangential.* Fusiform rays not numerous, broad and high, the cells of the inflated portion large and thin-walled, often much broken down. Ordinary rays low to medium, strongly resinous, when of a few elements

only, wholly composed of tracheids; much contracted at the position of the often interspersed and very narrow tracheids; the parenchyma cells unequal, oval, and somewhat variable; the thin lateral walls strongly incurved or convex, sometimes much inflated.

A large tree 30-46 m. in height, with a trunk upwards of 1.50 m. in diameter.

Wood very light, soft, not strong, close and straight grained, and compact.

Specific gravity . . . . .	0.3908
Percentage of ash residue . . . . .	0.23
Approximate relative fuel value . . . . .	38.99
Coefficient of elasticity in kilograms on millimeters . . . . .	950.
Ultimate transverse strength in kilograms . . . . .	260.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5349.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1071.
(Sargent)	

A somewhat uncommon but valuable timber tree, usually below 3000 feet elevation in British Columbia, but rising to 7000-10,000 feet in California. Cœur D'Alène and Bitter Root Mountains of Idaho, to the valley of the Flathead River, northern Montana; south along the Cascade Mountains of Washington and Oregon, and the California Sierras to Calaveras County (Sargent); Vancouver Island; the Gold and Coast ranges of British Columbia, disappearing at an elevation of 2235 feet (Macoun).

## 9. *P. flexilis*, James

### *White Pine*

*Transverse.* Growth rings narrow, rather uniform. Summer wood very thin, of 3-4 tracheids and open, the tracheids large, squarish, uniform. Spring wood very open, the tracheids squarish, rather variable, the walls thin. Medullary rays not prominent or numerous, 1 cell wide, distant 2-8 rows of tracheids. Resin passages large, numerous, the epithelium very thin-walled.

*Radial.* Rays nonresinous; the low, marginal, and sparingly interspersed tracheids rather numerous. Parenchyma ray cells straight; the upper and lower walls with frequent, broad pits; the terminal walls thin and not pitted; the lateral walls with large, oval, or oblong-lenticular pits, 1-2, or in the marginal cells more rarely 3-4, per tracheid, in the summer wood reduced to 1 and lenticular. Bordered pits elliptical, large, in 1 row, rather numerous. Pits on the tangential walls of the summer wood numerous and prominent, broadly lenticular, especially numerous on the outermost wall, becoming scattering within. Resinous tracheids wanting.

*Tangential.* Fusiform rays few, rather high and broad, the cells of the inflated portion very thin-walled and often completely broken out. Ordinary rays numerous, medium, nonresinous, not conspicuously

contracted by the sparingly interspersed tracheids; the cells equal, oval, and uniform, thin-walled; the lateral walls not concave or convex.

A tree 15-18 m. high, with a trunk upwards of 1.20 m. in diameter.

Wood light, soft, close grained, and compact.

Specific gravity . . . . .	0.4358
Percentage of ash residue . . . . .	0.28
Approximate relative fuel value . . . . .	43.42
Coefficient of elasticity in kilograms on millimeters . . . . .	676.
Ultimate transverse strength in kilograms . . . . .	266.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5591.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1727.

(Sargent)

Rocky Mountains of British Columbia (Macoun); southward through the Rocky Mountains to Utah, Nevada, New Mexico, and Texas; Inyo Mountains and Mount Silliman, California (Sargent).

#### 10. *P. reflexa*, Engelm.

##### *White Pine*

*Transverse.* Growth rings variable, often double. Summer wood conspicuous but thin or upwards of one half the spring wood, from which the transition is gradual, the structure open. Spring tracheids large, squarish-hexagonal, the walls rather thickish, conspicuously unequal, and often in irregular rows. Medullary rays not very broad, 1 cell wide, distant 2-10 rows of tracheids, somewhat prominent; the side walls of the cells conspicuously inflated and projecting into the adjacent tracheid cavities. Resin passages numerous and large, chiefly in or near the summer wood; the epithelium composed of large and thin-walled, very resinous cells; when in the summer wood the resin passage is central to a large tract of thin-walled tracheids.

*Radial.* Rays nonresinous; the tracheids numerous, low, marginal, and sparingly interspersed. Parenchyma ray cells straight; the upper and lower walls rather thickish and entire or again somewhat strongly pitted, especially in the summer wood; the terminal walls thin and entire or locally thickened; the lateral walls with large, oval, or squarish pits which finally become lenticular, 1-2, chiefly 1, per tracheid throughout. Bordered pits numerous, elliptical, in 1 row, distinctly smaller and round toward the summer wood where the orifice becomes a more or less extended slit merging into double striations. Pits on the tangential walls of the summer wood rather small and flat, narrowly lenticular, chiefly confined to the outermost wall where they are rather numerous. Resinous tracheids wanting.

*Tangential.* Fusiform rays broad, rather numerous, the cells of the inflated portion very large, thin-walled. Ordinary rays medium to low, not very numerous, nonresinous, rarely contracted by smaller, interspersed tracheids; the parenchyma cells equal, oval, or oblong, the thin side walls strongly inflated, more rarely incurved.

A tree 24-30 m. high, with a trunk sometimes exceeding .60 m. in diameter. Wood light, hard, not strong, close grained, and compact.

Specific gravity . . . . .	0.4877
Percentage of ash residue . . . . .	0.26
(Sargent)	

Rocky ridges and slopes of almost inaccessible cañons at elevations between 6000 and 8000 feet. High mountains of southeastern New Mexico, to the Santa Rita Mountains and the Santa Catalina Mountains of Arizona (Sargent).

# 11. \* *P. strobus*, Linn.

## *White Pine. Weymouth Pine*

*Transverse.* Growth rings usually thick. Summer wood usually thin, of about 8 tracheids, rather conspicuous, variable and rather open, sometimes double; the tracheids squarish, unequal in regular rows, the transition from the spring wood gradual. Spring wood open, the rather large but very unequal tracheids distinctly hexagonal and thin-walled. Medullary rays not very prominent or broad, 1 cell wide, few, distant 2-16, or more rarely 20, rows of tracheids. Resin passages numerous, medium, the epithelium sparingly resinous.

*Radial.* Rays nonresinous, the tracheids long and low, numerous, marginal and sparingly interspersed when they are very low. Parenchyma ray cells straight, equal to 6-15 spring tracheids; the upper and lower walls rather thickish and entire or distantly pitted; the terminal walls thin and entire or somewhat locally thickened; the lateral walls with very large, oval, or lenticular pits 1-2 per tracheid throughout, more rarely 3 per tracheid. Bordered pits rather numerous in 1 row, large, strongly elliptical, much reduced, and finally obscure in the summer wood where the orifice becomes a prolonged, diagonal slit. Pits on the tangential walls of the summer wood numerous but small, chiefly narrowly lenticular. Resinous tracheids wanting.

*Tangential.* Fusiform rays few, not very broad, nonresinous; the cells of the inflated portion large and thin-walled, often much broken out, or in small branches often wholly wanting. Ordinary rays low to medium, not very numerous, narrow, nonresinous; the cells equal, rather uniform, oblong, narrow, the side walls rarely convex, more generally concave.

A large tree of the greatest economic value, 24-52 m. high, with a trunk upwards of 3.50 m. in diameter.

Wood light, soft, not strong, very close and straight grained, compact, easily worked, and susceptible of a beautiful polish.

Specific gravity . . . . .	0.3854
Percentage of ash residue . . . . .	0.19
Approximate relative fuel value . . . . .	38.47
Coefficient of elasticity in kilograms on millimeters . . . . .	851.
Ultimate transverse strength in kilograms . . . . .	267.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6219.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1194.
(Sargent)	



The following determinations are after Bovey:

Coefficient of strength in pounds for:

Bending . . . . .	4,800
Torsion . . . . .	10,000
Compression . . . . .	3,500
Shear . . . . .	340
Weight per cubic foot . . . . .	26

One of the most valuable and widely spread trees of Canada, extending from Newfoundland, Anticosti, Nova Scotia, and New Brunswick throughout Quebec and Ontario, and westward nearly to Lake Winnipeg (Macoun); southward through the northern United States to Pennsylvania, the southern shores of Lake Michigan; La Salle, Illinois; Davenport, Iowa; along the Allegheny Mountains to northern Georgia (Sargent).

Pleistocene deposits of the Don Period, Toronto.

Material preserved in natural state, but showing the effects of extended decay.

## 12. *P. parviflora*, Sieb. et Zucc.

*Jap.* = *Himekomatsu*

*Transverse.* Growth rings rather broad, the usually thin summer wood upwards of one half the spring wood, from which the transition is gradual. Summer wood rather open, often double, the tracheids conspicuously unequal, rounded-hexagonal. Spring tracheids rather large, squarish, uniform, in regular rows, rather thin-walled, radially elongated. Medullary rays not prominent or numerous, very narrow, 1 cell wide, distant 2-10 rows of tracheids. Resin passages large, rather numerous, the epithelium composed of large and thin-walled cells.

*Radial.* Rays nonresinous; the tracheids low, marginal, rarely interspersed. Parenchyma ray cells straight, equal to about 5-7 spring tracheids; the upper and lower walls very variable, chiefly rather thin, often distantly and obscurely pitted; the terminal walls thin and not pitted; the lateral walls with large, oval, or radially elongated simple pits, 1, or in the early spring wood 2, per tracheid, in the summer wood becoming vertically lenticular. Bordered pits very large and narrowly elliptical, rather numerous, in 1 row. Pits on the tangential walls of the summer wood small, rather few and widely scattering, except on the outermost wall. Resinous tracheids apparently wanting.

*Tangential.* Fusiform rays broad, the large resin canal with prominent thyloses and thin epithelium cells, the cells of the inflated portion all thin-walled. Ordinary rays narrow, conspicuously contracted at the position of the much narrower, occasionally interspersed tracheids; the parenchyma cells chiefly equal, rather thin-walled, somewhat variable, chiefly oblong and narrow or sometimes oval and much broader, but uniform in the same ray, the lateral walls concave, more rarely convex. Resinous tracheids sparingly present, the resin in plates simulating Sanio's bands.

13. *P. albicaulis*, Engelm.*White Pine*

**Transverse.** Growth rings medium, uniform. Summer wood very thin and open, the tracheids in regular rows, squarish, the transition from the spring wood very gradual. Spring tracheids large, squarish-hexagonal, rather uniform in regular rows, rather thin-walled. Medullary rays rather broad, 1 cell wide, somewhat prominent, distant 2-8 rows of tracheids. Resin passages medium, rather numerous, the prominent and somewhat resinous epithelium composed of large and thin-walled cells. Resinous tracheids often present but not prominent, forming radial series contiguous to the medullary rays.

**Radial.** Rays nonresinous; the tracheids long and low, marginal, rarely interspersed. Parenchyma ray cells straight; the upper and lower walls medium, variable, and with variable, often distant but chiefly broad pits; the terminal walls thin and not pitted; the lateral walls with large, oval, or broadly lenticular pits, 1-2, chiefly 1, per tracheid throughout. Bordered pits numerous, large, round, in 1 row. Pits on the tangential walls of the summer wood not very numerous, rather small and flat, chiefly on the outermost walls. Resinous tracheids somewhat numerous and prominent, the resin forming plates opposite the medullary rays and simulating Sanio's bands.

**Tangential.** Fusiform rays high, rather narrow, the cells of the inflated portion medium to small and thin-walled. Ordinary rays rather numerous, medium, nonresinous, somewhat contracted at the position of the occasionally interspersed and rather narrower tracheids; the cells rather equal and oval or oblong, the walls thin, often concave, more rarely convex. Resinous tracheids somewhat prominent, the resin in plates simulating Sanio's bands.

A small Alpine tree, 6-12 m. high, with a trunk rarely .60 m. in diameter. Wood light, soft, not strong, brittle, close grained, and compact.

Specific gravity . . . . .	0.4165
Percentage of ash residue . . . . .	0.27
Approximate relative fuel value . . . . .	41.54
Coefficient of elasticity in kilograms on millimeters . . . . .	512.
Ultimate transverse strength in kilograms . . . . .	249.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5296.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1716.
(Sargent)	

Rocky Mountains of British Columbia between 6000 and 7000 feet elevation, northward to latitude 53° (Macoun); Cascade and Blue mountains of Washington and Oregon; Scott's Mountain, Mt. Shasta, and the high peaks of the Sierra Nevadas to Mt. San Bernardino, California. Dry, gravelly ridges at the extreme limit of growth, in the San Bernardino Mountains attaining an elevation of 10,500 feet, and at the highest elevations becoming a prostrate shrub (Sargent).

*Section II. Hard Pines.***14. *P. clausa*, Sarg.***Sand Pine. Scrub Pine. Spruce Pine*

*Transverse.* Growth rings thick, often double. Summer wood dense, rarely somewhat open, often exceeding the spring wood, from which the transition is usually very abrupt, and within the same section showing both open and dense structure; the tracheids rounded, unequal, and often in irregular rows. Spring tracheids hexagonal, not very uniform, the walls rather thickish. Resin passages large, chiefly in the summer wood; the epithelium composed of large, round, and thin-walled cells chiefly in 1 row, occasionally in 2 rows and forming more or less eccentric tracts. Medullary rays not very prominent or broad, 1 cell wide, distant 2-8 rows of tracheids.

*Radial.* Rays nonresinous; the tracheids often predominant and when interspersed often becoming very low, strongly reticulated throughout. Ray cells of one kind only, the cells rather broad, long fusiform; the terminal walls thin and entire; the upper and lower walls very thin; the lateral walls with very variable, lenticular, or oval pits, 1-5, chiefly 2-3, per tracheid, in the summer wood reduced to 1. Bordered pits conspicuously in 1-2 rows, elliptical, in the summer wood abruptly reduced to  $14.4\ \mu$ , and finally to  $7.2\ \mu$ . Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays medium to high, rather broad; the terminals acute, somewhat prolonged, and composed of few tracheids; the inflated portion composed of very large, rounded, and usually extremely thin-walled cells among which there may be an occasional tracheid. Ordinary rays numerous and presenting three principal aspects: (1) low rays with large oval, central parenchyma cells and small, terminal tracheids, fusiform; (2) higher rays composed of large, squarish-celled and thin-walled parenchyma, with a few narrower, terminal tracheids; and (3) the highest rays composed of large, thin-walled, oval, and broad parenchyma cells with small terminal and smaller interspersed tracheids causing local contractions.

A tree 21-24 m. high, with a trunk upwards of .75 m. in diameter.

Wood light, soft, not strong, brittle.

Specific gravity . . . . .	0.5576
Percentage of ash residue . . . . .	0.31
Approximate relative fuel value . . . . .	55.09
Coefficient of elasticity in kilograms on millimeters . . . . .	543.
Ultimate transverse strength in kilograms . . . . .	214.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6028.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2100.
(Sargent)	

Barren, sandy dunes and ridges of Florida; shores of Pensacola Bay and southward within 30 miles of the coast to Pease Creek; on the east coast occupying a narrow ridge south of St. Augustine (Sargent).

15. *P. rigida*, Mill.*Pitch Pine*

*Transverse.* Growth rings thick. Summer wood dense, sometimes rather open, very prominent, often double, the transition from the spring wood gradual or somewhat abrupt; the tracheids rounded, not uniform, in rather irregular rows. Spring tracheids large, squarish-hexagonal, very unequal in regular rows. Resin passages large and numerous, chiefly in the summer wood; the epithelium in 1-2 rows of large, irregularly rounded, thin-walled, and often resinous cells which sometimes become thicker-walled in the outer limits, forming more or less extensive tracts eccentrically developed about the canal. Medullary rays rather prominent but few, distant 2-16, rarely 27, rows of tracheids. This wood shows a strong tendency to radial fracture.

*Radial.* Rays nonresinous; the tracheids strongly reticulated throughout, sparingly interspersed, very low, not conspicuously predominant. Ray cells of one kind, rarely of two kinds, chiefly low and long fusiform; the terminal, upper, and lower walls very thin and usually much broken out; the lateral walls with very variable, lenticular, or oval pits: (1) upwards of 6 per tracheid; and (2) 1-3, chiefly 2, per tracheid, usually becoming more prominent in the low rays, and in the summer wood often distinctly bordered, or again simple and very variable, often large. Bordered pits in 1 row or pairs, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not very numerous, rather low and broad; the terminals acute and composed of a few small tracheids; the cells of the inflated portion very thin-walled and large, but usually much broken out. Ordinary rays chiefly rather low and presenting two principal aspects: (1) low rays composed of thin-walled parenchyma much broken out, and a few small, terminal tracheids; and (2) higher rays of similar parenchyma cells with small, terminal, and few interspersed tracheids, the latter causing local contractions.

A tree 12-24 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, soft, not strong, brittle, coarse grained, and compact.

Specific gravity . . . . .	0.5151
Percentage of ash residue . . . . .	0.23
Approximate relative fuel value . . . . .	51.39
Coefficient of elasticity in kilograms on millimeters . . . .	581.
Ultimate transverse strength in kilograms . . . . .	316.
Ultimate resistance to longitudinal crushing in kilograms .	5687.
Resistance to indentation to 1.27 mm. in kilograms . . . .	2123.
(Sargent)	

Valley of the St. John River, New Brunswick, to the northern shores of Lake Ontario (Macoun); south through the Atlantic states to Georgia; westward to the western slopes of the Allegheny Mountains of West Virginia and Kentucky (Sargent).

16. *P. serotina*, Michx.*Pond Pine. Marsh Pine*

*Transverse.* Growth rings thick. Summer wood dense or in the narrow rings rather open, often exceeding the spring wood, from which the transition is commonly very abrupt; the tracheids large and not very uniform, hexagonal, in very regular rows. Spring tracheids large, squarish, the walls thin. Resin passages numerous and large, chiefly in the summer wood; the epithelium in 1-several rows of very large, round, and dark resinous cells, forming an extensive tract which is often strongly eccentric to the canal. Medullary rays prominent, broad, 1 cell wide, more or less resinous, distant 2-8 rows of tracheids.

*Radial.* Rays more or less resinous throughout; the tracheids commonly predominant, very variable in height, strongly reticulated throughout, sparingly interspersed. Ray cells of one kind only, chiefly rather high, more or less fusiform, equal to 4-6 spring tracheids, resinous; the terminal, upper, and lower walls thin and usually much broken out; the lateral walls with very variable, lenticular pits, 1-4, rarely 5, per tracheid, becoming very narrow and much prolonged slits in the summer wood. Bordered pits in 1 row or somewhat frequently in pairs, and thus more or less 2-rowed, round, or elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, resinous, narrow, medium to high, the terminals acute, more rarely prolonged, and composed of small tracheids; the inflated portion composed of large, thin-walled cells usually much broken out. Ordinary rays medium, numerous, broad, resinous, and presenting three principal aspects: (1) low rays of 1-several thin-walled, resinous parenchyma cells with small, terminal tracheids; (2) higher rays chiefly composed of very large, oblong, and often strongly reticulated tracheids with 1 or 2 large, resinous parenchyma cells much broken out; and (3) the highest rays of several oblong, resinous parenchyma cells with few terminal tracheids, or again variously contracted through the presence of small, interspersed tracheids. •

A tree 12-24 m. high, with a trunk upwards of .90 m. in diameter.

Wood heavy, soft, not strong, brittle, coarse grained, and compact.

Specific gravity . . . . .	0.7942
Percentage of ash residue . . . . .	0.17
Approximate relative fuel value . . . . .	79.29
Coefficient of elasticity in kilograms on millimeters . . . . .	1170.
Ultimate transverse strength in kilograms . . . . .	497.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	8079.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	4740.
(Sargent)	

An uncommon species in low, peaty soil, ponds, and along the borders of streams. North Carolina and south near the coast to the head of the St. John's River, Florida (Sargent).

**17. P. Banksiana, Lamb.***Scrub Pine. Gray Pine. Jack Pine*

**Transverse.** Growth rings narrow, uniform. Summer wood dense, about one half the spring wood, from which the transition is generally abrupt; the tracheids in regular rows, rather uniform. Spring tracheids conspicuously squarish, uniform in regular rows, the walls thin. Resin passages rather small, rather numerous, widely scattering; the epithelium in 1-2 rows of thin-walled cells, those of the first row much flattened, those of the second row large, irregularly rounded and resinous, with an occasional thick-walled cell, the whole forming an eccentric tract. Medullary rays not very broad, somewhat prominent, distant 2-10 rows of tracheids.

**Radial.** Rays sparingly resinous; the ray tracheids strongly predominant and for the most part strongly reticulated throughout, interspersed. Ray cells of 1 kind only, short fusiform and equal to about 4 spring tracheids; the terminal walls thin and not pitted; the upper and lower walls variable, sometimes very thin and entire, or again thicker and unequal; the lateral walls with very irregularly oval or lenticular and unequal pits, 1-6 per tracheid, in the summer wood becoming 1. Bordered pits in 1 row, sometimes in pairs or again distinctly 2-rowed, elliptical, becoming smaller and more distant toward the summer wood, where they are quickly reduced and are finally obscure or wanting. Pits on the tangential walls of the summer wood wholly wanting.

**Tangential.** Fusiform rays rather low and narrow, rather few; the terminals acute or somewhat prolonged and chiefly composed of tracheids; the cells of the inflated portion large and rather thin-walled, generally all present. Ordinary rays low and chiefly narrow, presenting three principal aspects: (1) low rays composed of oblong or narrowly oval, thin-walled parenchyma cells with narrowly oblong, terminal tracheids; (2) low rays of similar composition, but the parenchyma cells much thinner-walled; and (3) the highest rays composed chiefly of narrow tracheids with a few broader, oblong parenchyma cells interspersed.

A small tree 9-22 m. high, with a trunk rarely exceeding .75 m. in diameter. Wood light, soft, not strong, rather close grained, and compact.

Specific gravity . . . . .	0.4761
Percentage of ash residue . . . . .	0.23
Approximate relative fuel value . . . . .	47.50
Coefficient of elasticity in kilograms on millimeters . . . . .	942.
Ultimate transverse strength in kilograms . . . . .	278.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6329.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1609.
(Sargent)	

Halifax, Nova Scotia, northwesterly to the Athabasca River and down the Mackenzie River to the Arctic Circle; eastward it hardly becomes a tree, but westward it increases in size, and westward of Lake Winnipeg it

equals the red pine of the east in height and diameter (Macoun); southward through northern Maine; at Ferrisburg, Vermont; thence westward along the southern shores of Lake Michigan to central Minnesota. Barren, sandy soil, more rarely in rich loam (Sargent).

### 18. *P. contorta*, Loud.

#### *Scrub Pine*

*Transverse.* Growth rings thick. Summer wood dense, conspicuous, often exceeding the spring wood; the tracheids in regular rows, those in the outer portion generally much compressed, variable, those of the central portion more uniform and with rounded lumens; transition from the spring wood gradual. Spring tracheids hexagonal, unequal, in regular rows, the walls rather thin. Resin passages scattering, numerous, small; the epithelium in 1-3 rows of angular, thin-walled cells which merge outwardly into thicker-walled elements, the whole forming an irregular and somewhat extended tract. Medullary rays rather narrow, 1 cell wide, not prominent, rather numerous, distant 2-12 rows of tracheids.

*Radial.* Rays nonresinous; the tracheids numerous, low, sparingly interspersed and sometimes predominant, distinctly reticulated throughout. Ray cells of one kind only and variously fusiform; the terminal, upper, and lower walls very thin and often much broken out or wholly wanting; the lateral walls with large, oblong, or lenticular pits which often become round or oval when the ray is only 1 cell high, and on the inner face of the spring wood in all rays, 1-4, chiefly 2-3, per tracheid, in the summer wood greatly reduced in size, shape, and number. Bordered pits in 1 row, sometimes in pairs, elliptical, becoming much reduced and remote in the summer wood. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not numerous, medium; the terminals acute, rarely somewhat prolonged, and composed of small tracheids; the cells of the inflated portion all very thin-walled and generally broken out. Ordinary rays medium, rather numerous, the thin-walled parenchyma cells predominant, commonly broken out so as to leave the ray vacant for nearly the whole height, the tracheids chiefly terminal but occasionally interspersed as somewhat narrower and rounded elements, causing local but slight contraction.

A small, stunted tree 6-9 m. high, with a trunk upwards of .50 m. in diameter. Wood light, hard, strong, brittle, and coarse grained.

Specific gravity . . . . .	0.5815
Percentage of ash residue . . . . .	0.19
Approximate relative fuel value . . . . .	58.04
Coefficient of elasticity in kilograms on millimeters . . . . .	1585.
Ultimate transverse strength in kilograms . . . . .	423.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	8868.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2382.
(Sargent)	

Sandy dunes and exposed rocky points, everywhere on the coast of British Columbia; when sheltered growing in groves; rarely found in the Queen Charlotte Islands (Macoun); Alaska and southward from British Columbia along the coast to Mendocino County, California, and inland to the western slopes of the coast ranges (Sargent).

19. *P. glabra*, Walt.

*Cedar Pine. Spruce Pine. White Pine*

*Transverse.* Growth rings thick. Summer wood of about one half the spring wood, from which the transition is usually somewhat abrupt, double or treble, the central portions dense, the outer portions open, especially when double or treble; the tracheids rather variable, in regular rows. Spring tracheids hexagonal, uniform in regular rows, the walls thin. Resin passages rather abundant, medium; the epithelium in 1-2 rows of large, rounded and thin-walled, resinous and irregular cells usually much broken out, but not forming very extended tracts. Medullary rays not very broad, prominent, or numerous, distant 2-12 rows of tracheids.

*Radial.* Rays very sparingly resinous, the tracheids sparingly reticulated, often predominant and interspersed. Ray cells of two kinds: (1) rather rare; and (2) the terminal, upper, and lower walls very thin and often apparently wanting; the lateral walls with lenticular, variable pits, 1-6, chiefly 2 or 3, per tracheid, in the summer wood finally reduced to 1 and becoming a short slit. Bordered pits in 1 row, elliptical, in the summer wood soon reduced to  $9.6\ \mu$ , the orifice often much prolonged, sometimes rather large and bordered. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not numerous, medium; the terminals acute, or slightly prolonged and composed of small tracheids; the inflated portion composed of thin-walled cells all broken out. Ordinary rays chiefly low to medium, somewhat numerous, and presenting two principal aspects: (1) rays composed of large, thin-walled parenchyma cells much broken out, and few, small, terminal tracheids; and (2) rays composed of large, thin-walled parenchyma cells with terminal and interspersed, chiefly predominant and narrower, tracheids causing local contraction.

A tree 24-30 m. high, with a trunk upwards of 1.20 m. in diameter.

Wood light, soft, not strong, brittle, very coarse grained, not durable.

Specific gravity . . . . .	0.3931
Percentage of ash residue . . . . .	0.45
Approximate relative fuel value . . . . .	39.13
Coefficient of elasticity in kilograms on millimeters . . . . .	448.
Ultimate transverse strength in kilograms . . . . .	212.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4604.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1694.
(Sargent)	



South Carolina to the Chattahoochee region of Florida, chiefly near the coast, thence through the Gulf States south to latitude  $32^{\circ} 30'$  to the valley of the Pearl River, Louisiana, its greatest development being in Alabama and Mississippi (Sargent).

## 20. *P. echinata*, Mill.

*Yellow Pine. Short-Leaved Pine*

*Transverse.* Growth rings thick. Summer wood thick, very prominent, dense, and often exceeding the spring wood from which the transition is generally very abrupt; the tracheids unequal in regular rows, but varying greatly in different growth rings so that the structure presents a very variable density. Spring tracheids large, squarish-hexagonal, the walls thin. Resin passages numerous but large and scattering; the epithelium composed of 1 row of thin-walled cells, less frequently becoming 2-rowed in part, the cells often resinous. Medullary rays prominent, rather broad, numerous, distant 2-8 rows of tracheids.

*Radial.* Rays somewhat resinous throughout; the ray tracheids rather high, conspicuously predominant and very strongly reticulated throughout, often composing the entire ray. Ray cells of one kind, rarely of two kinds, few, interspersed, fusiform; the terminal, upper, and lower walls very thin and much broken out; the lateral walls with very variable, lenticular pits, 1-4 per tracheid, becoming more or less obsolete in the summer wood. Bordered pits in 1 row or pairs, rarely 2-rowed, elliptical, in the summer wood reduced to  $7.2 \mu$ , when the orifice often becomes obscure or eccentric. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, high, the terminals prolonged, linear, and composed of broad parenchyma cells with terminal tracheids; the cells of the inflated portion very thin-walled and usually all broken out. Ordinary rays rather numerous, high, presenting two principal aspects: (1) low rays composed of thin-walled parenchyma much broken out, and small, terminal tracheids; and (2) higher rays composed of oblong tracheids with few, interspersed, broader cells of thin-walled parenchyma, thus causing local expansions.

A tree 24-30 m. in height, with a trunk upwards of 1.35 m. in diameter.

Wood varying greatly, heavy, hard, strong, generally coarse grained, and compact.

Specific gravity . . . . .	0.6104
Percentage of ash residue . . . . .	0.29
Approximate relative fuel value . . . . .	60.86
Coefficient of elasticity in kilograms on millimeters . . . . .	1375.
Ultimate transverse strength in kilograms . . . . .	443.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7628.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2064.

(Sargent)

Staten Island, New York, thence southward to western Florida and through the Gulf States to Tennessee and eastern Texas; through Arkansas to Oklahoma; southeastern Kansas, southern Missouri, and in Union County, Illinois (Sargent).

## 21. *P. resinosa*, Ait.

*Red Pine. Norway Pine*

*Transverse.* Growth rings very thick, often double. Summer wood about one fifth the spring wood, from which the transition is very gradual; not very dense, but when double the outer band is generally more open with the tracheids less compressed, the inner band is more dense with the tracheids usually thick-walled and more conspicuously compressed; the tracheids round-hexagonal, conspicuously unequal in regular rows, the walls rather thick. Spring tracheids hexagonal, uniform in regular rows, the walls thickish. Resin passages very scattering, not numerous, large; the epithelium not extensive, about 2 layers thick, the cells of the layer next the canal radially flattened, those of the other layers oval, often resinous. Medullary rays rather prominent and broad, numerous, distant 2-9 rows of tracheids.

*Radial.* Rays nonresinous, the ray tracheids low, marginal, rarely interspersed, conspicuously dentate. Ray cells long and low, straight, or in the summer wood often conspicuously contracted at the ends; the terminal walls thin and entire; the upper and lower walls rather thin, remotely and imperfectly pitted; the lateral walls with very large, oval or oblong, very variable pits, which become lenticular toward the summer wood, 1-2, chiefly 1, per tracheid throughout. Bordered pits in 1 row, sometimes in pairs, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not numerous, chiefly rather low and broad, the cells rather large and thin-walled throughout. Ordinary rays medium, nonresinous, numerous, rarely contracted by much smaller and narrower, interspersed tracheids; the cells chiefly equal but not very uniform, oval or squarish, rather large, and thin-walled, the lateral walls very thin and chiefly concave.

A tree 24-46 m. high, with a trunk upwards of 1.37 m. in diameter. Wood light, not strong, hard, rather coarse grained, and compact.

Specific gravity . . . . .	0.4854
Percentage of ash residue . . . . .	0.27
Approximate relative fuel value . . . . .	48.41
Coefficient of elasticity in kilograms on millimeters . . . . .	1132.
Ultimate transverse strength in kilograms . . . . .	341.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	7274.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1353.
(Sargent)	

The following determinations are after Bovey :

Coefficient of strength in pounds for :

Bending . . . . .	5,400
Elasticity . . . . .	1,430,000
Torsion . . . . .	11,500
Compression . . . . .	3,900
Shear . . . . .	380
Weight per cubic foot . . . . .	33

Rather a widely distributed but somewhat localized tree flourishing particularly in the poorest soils ; Nova Scotia, New Brunswick, Quebec, and westward to Lake of the Woods (Macoun) ; through the New England States to northern Pennsylvania and westward to Michigan and central Minnesota (Sargent).

## 22. *P. tropicalis*, Morelet

*Transverse.* Growth rings narrow, unequal. Summer wood chiefly rather dense but somewhat variable, usually exceeding the spring ; the tracheids hexagonal-oblong, uniform, and in regular rows ; transition from the spring wood abrupt or more rarely gradual. Spring tracheids large, conspicuously squarish or hexagonal, the walls rather thin. Medullary rays prominent, resinous, 1 cell wide, broad, distant 2-8, or more rarely 12, rows of tracheids. Resin passages numerous, large, resinous, and chiefly confined to the summer wood ; the epithelium of 1-2 rows of thin-walled cells which often form tangentially extended tracts.

*Radial.* Ray tracheids rather low and rather sparingly dentate, never reticulate ; numerous and interspersed, often predominant. Medullary rays resinous, the cells all of one kind ; the upper, lower, and terminal walls thin and commonly much broken down ; the side walls with large, oval, oblong, or lenticular pits, 1-2, chiefly 1, per tracheid, in the summer wood often reduced and vertically lenticular. Pits on the tangential walls of the summer tracheids wholly wanting, but often appearing on the tangential walls of the first spring tracheid. Bordered pits large, in 1 row or in pairs, the latter often approximating so as to form 2 rows ; in the summer wood becoming much reduced and rather distant in 1 row.

*Tangential.* Fusiform rays somewhat numerous, medium ; the terminals somewhat prolonged but usually acute and composed of few, thick-walled tracheids ; the cells of the central tract all thin-walled and much broken out. Ordinary rays numerous, very resinous, medium ; the cells oval, uniform, and equal but much broken out ; the higher rays somewhat contracted by the interspersed, rather smaller, and thick-walled tracheids.

Cuba and Isle of Pines, West Indies.

A careful comparison of this wood with that of *P. resinosa* will show that while they are very closely related, there are, nevertheless, essential structural differences which compel us to recognize them as distinct species.

23. *P. Thunbergii*, Parl.*Jap. = Kuromatsu*

*Transverse.* Growth rings rather broad, variable. Summer wood dense, sometimes equal to the spring wood from which the transition is abrupt, rarely gradual, often double; the rounded tracheids rather equal in regular rows. Spring tracheids large, hexagonal, unequal in regular rows, the walls rather thin. Resin passages rather numerous, rather large and scattering; the epithelium in 1-2 rows of very large and very thin-walled cells not extending much beyond the central canal; nonresinous; in the summer wood the layer next the canal is much compressed and the cells are barely recognizable. Medullary rays few, not very broad or prominent, distant 2-8 rows of tracheids.

*Radial.* Rays nonresinous; the ray tracheids more or less dentate but not reticulate, generally predominant and marginal, not interspersed. Ray cells of one kind only, straight; the terminal walls thin and entire; the upper and lower walls thickish and entire or distantly and obscurely pitted; the lateral walls with very large, oblong, or lenticular pits, almost strictly 1, rarely 2, per tracheid, in the summer wood becoming distinctly bordered, when they are broadly oval with a long, slitlike orifice. Bordered pits large, elliptical, not very numerous, in 1 row. Pits on the tangential walls wholly wanting.

*Tangential.* Fusiform rays rather numerous but low and broad, the chiefly rather short terminals wholly composed of small, oval tracheids, and a few parenchyma cells, the inflated portion composed of very thin-walled cells much broken out. Ordinary rays rather numerous, low to medium, nonresinous, not very broad but presenting two principal aspects: (1) narrow rays composed of a few central, oval parenchyma cells and several variable, terminal tracheids; and (2) broader rays composed of oval parenchyma cells and a few terminal and small tracheids.

24. *P. densiflora*, Sieb. et Zucc.*Jap. = Akamatsu*

*Transverse.* Growth rings very uniform. Summer wood one half the spring wood, from which the transition is abrupt, chiefly dense but somewhat variable, the tracheids rounded, unequal in regular rows. Spring tracheids hexagonal, rather uniform, in regular rows, the walls thickish. Resin passages numerous, large, scattering; the epithelium in 1-2 rows of thin- and thick-walled cells, easily broken out and generally wanting, nonresinous. Medullary rays few, not very prominent, very narrow, rather obscure, distant 2-20 rows of tracheids.

*Radial.* Rays nonresinous; the ray tracheids dentate, sparingly reticulate in the summer wood, usually predominant and marginal, sparingly interspersed. Ray cells of one kind only and straight; the terminal walls thin and entire; the upper and lower walls thin, somewhat uniform, not obviously pitted; the lateral walls with very large and

simple, oblong, or oval pits, almost strictly 1 per tracheid, in the summer wood distinctly bordered and then large, oval, with a broad, oblong orifice. Bordered pits large, elliptical, rather numerous, in 1 row. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, medium, narrow, the slightly prolonged terminals composed of a few small tracheids; the gradually inflated portion composed of very thin-walled cells all broken out. Ordinary rays medium, rather numerous, not very broad and presenting two principal aspects: (1) low to medium rays composed of 1-several oval parenchyma cells with small, terminal tracheids which often become predominant; and (2) the highest rays with numerous tracheids and few, interspersed parenchyma cells.

## 25. *P. Murrayana*, A. Murr.

*Black Pine. Lodge Pole Pine. Spruce Pine*

*Transverse.* Growth rings usually broad. Summer wood very thin, the structure very open throughout, the transition from the spring wood very gradual; the tracheids compressed, unequal, rather squarish, in somewhat irregular rows. Spring tracheids somewhat squarish-hexagonal, often in very irregular rows, unequal, the walls thin. Resin passages rather small and scattering; the epithelium in 1 row of very large and thin-walled, somewhat radially flattened, nonresinous cells, immediately inclosed by a layer of large, thin-walled tracheids. Medullary rays prominent, broad, 1 cell wide, numerous, distant 2-9, more rarely 11 rows, of tracheids.

*Radial.* Rays uniformly somewhat resinous throughout; the ray tracheids sparingly dentate, more or less reticulate in the summer wood, marginal and interspersed, often predominant. Ray cells apparently of two kinds, but merging so as to be more or less indistinguishable, strongly but variously fusiform; the terminal walls thin and entire or locally thickened; the upper and lower walls either entire or locally and irregularly thickened, thin; the lateral walls with rather small, round, oval, or lenticular pits, at first simple, but toward and in the summer wood with a more or less obvious border and oblong orifice, 1-4, rarely 5, per tracheid, in the summer wood reduced to 1-2. Bordered pits in 1 row, sometimes in pairs, not much crowded but strongly elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays low, few and small, rather broad, more or less unequal, acute or somewhat prolonged, the cells rather small and thick-walled throughout, the central tract usually much broken out. Ordinary rays numerous, broad, when a few cells high conspicuously fusiform; the high rays commonly contracted at the position of small and frequently interspersed tracheids; the parenchyma cells rather thin-walled, round, or transversely oval, very unequal and variable, the higher rays commonly showing smaller and thicker-walled cells either singly or in pairs.

A tree 18–24 m. high, with a trunk upwards of 1.20 m. in diameter.

Wood light, soft, not strong, close and straight grained, easily worked, compact, not durable.

Specific gravity . . . . .	0.4096
Percentage of ash residue . . . . .	0.32
Approximate relative fuel value . . . . .	40.83
Coefficient of elasticity in kilograms on millimeters . . . . .	771.
Ultimate transverse strength in kilograms . . . . .	241.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5328.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1379.
(Sargent)	

An Alpine tree somewhat localized in the Rocky Mountains of British Columbia at elevations of 3500–4000 feet, and northward to latitude 62° (Macoun); mountain ranges of Washington, Oregon, and the Sierra Nevadas of California to San Jacinto; southward through the mountains of Idaho, Montana, Wyoming, Colorado, and Utah to New Mexico and northern Arizona. The tree attains its greatest development in the California Sierras, in the interior occurring on dry, gravelly soil covering immense areas. In the Rocky Mountain region it occupies the borders of moist Alpine meadows between 6000 and 9000 feet elevation (Sargent).

## 26. *P. arizonica*, Engelm.

### *Yellow Pine*

*Transverse.* Growth rings chiefly thick but variable, often double. Summer wood thin, of about 4–10 tracheids but very variable, usually very open; the tracheids very unequal, now small and round or again large and much compressed, often in very irregular rows; transition from the spring wood somewhat gradual. Spring tracheids large, hexagonal, uniform, in regular rows, the walls thin. Resin passages very large, rather abundant; the epithelium in 2 rows, that next the canal composed of large and rather thin-walled cells which are immediately bounded by a layer of rather thick-walled, large, rounded, and often resinous cells. Medullary rays broad, 1 cell wide, rather prominent, sparingly and locally resinous, distant 2–10 rows of tracheids.

*Radial.* Rays locally resinous; the ray tracheids strongly predominant, strongly dentate, and somewhat reticulated in the summer wood. Ray cells sparingly fusiform and of two kinds: (1) rather numerous, the terminal walls thin and entire; the upper and lower walls rather thick and very coarsely pitted; the lateral walls with variously oval, oblong, or lenticular pits, 2–4, chiefly 4, per tracheid, becoming 2 in the summer wood; (2) the cells equal to about 5 spring tracheids, the terminal walls thin and entire; the upper and lower walls thin and entire; the lateral walls with oval, oblong, or round pits, 2–4, chiefly 4, per tracheid, becoming 2 in the summer wood. Bordered pits in 1 row, sometimes in pairs, often numerous, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous and narrow, the terminals somewhat prolonged but rather broad, the cells of the inflated portion rather thick-walled, those of the terminals large and thin-walled. Ordinary rays rather numerous, low to medium, much narrowed by the numerous and very variable, interspersed, and predominant tracheids; the relatively few parenchyma cells often resinous, very unequal and variable, oval, both thick- and thin-walled, the latter often much broken out.

A large tree 61-91 m. high, with a trunk 3.60-4.57 m. in diameter.

Wood variable in quality and value, hard, heavy, strong, brittle, not coarse grained nor durable, compact.

Specific gravity . . . . .	0.4715
Percentage of ash residue . . . . .	0.35
Approximate relative fuel value . . . . .	50.28
Coefficient of elasticity in kilograms on millimeters . . . . .	824.
Ultimate transverse strength in kilograms . . . . .	279.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6292.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1740.

(Sargent)

Interior of British Columbia south of latitude 51°, thence southward along the mountain ranges of the Pacific region to Mexico; eastward to the Black Hills of Dakota, Colorado, and western Texas. Dry, rocky ridges and prairies, or in the northern portion of California, rarely in cold, wet swamps, reaching its greatest development on the western slopes of the California Sierras (Sargent).

## 27. P. Coulteri, D. Don

### *Pitch Pine*

*Transverse.* Growth rings thick, variable. Summer wood thin, upwards of 10 tracheids and open, the transition gradual; the tracheids very variable, rounded, and often much compressed, in conspicuously irregular rows. Spring tracheids large, squarish-hexagonal, the walls rather thin. Resin passages rather abundant, medium; the epithelium in 1-several rows of large, rather thick-walled, and chiefly rounded cells, nonresinous, often forming extensive and irregular tracts about the canal. Medullary rays broad, 1 cell wide, rather prominent, distant 2-20 rows of tracheids.

*Radial.* Rays sparingly resinous throughout; the tracheids low, often predominant, more or less reticulated throughout, and often composing the entire structure in low rays. Parenchyma cells fusiform, of two kinds: (1) high and prominent, especially in the low rays; the terminal walls thin and not pitted; the upper and lower walls thick and coarsely pitted; the lateral walls with round or oval and prominent pits, 1-4, more rarely 6, per tracheid, becoming 1-2 in the summer wood; and (2) the cells fusiform, the terminal walls thin and not pitted; the upper and lower walls very thin, often much broken out, or again

somewhat thickened, and thus passing into cells of the first order; the lateral walls with oval or lenticular pits, 1-3, chiefly 2, per tracheid throughout, very unequal and variable in form and size. Bordered pits in 1 row, sometimes in pairs, elliptical, becoming greatly reduced in the summer wood, and finally wanting. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, medium, narrow; the acute or rarely prolonged terminals almost wholly composed of tracheids; the cells of the inflated portion very thin-walled and usually broken out. Ordinary rays rather numerous, low to high, nonresinous and presenting three principal aspects: (1) low rays wholly composed of tracheids and thick-walled parenchyma cells, rarely 2-seriate, at least in part; (2) 1-seriate rays with the thin-walled parenchyma of the central portion much broken out, and showing an interspersed thick-walled parenchyma cell near the center; and (3) 1-seriate rays chiefly composed of thin-walled parenchyma terminated above and below by thick-walled cells and tracheids.

A tree 24-26 m. high, with a trunk upwards of 1.80 m. in diameter.

Wood light, soft, not strong, brittle, and coarse grained.

Specific gravity . . . . .	0.4133
Percentage of ash residue . . . . .	0.37
Approximate relative fuel value . . . . .	41.18
Coefficient of elasticity in kilograms on millimeters . . . . .	1141.
Ultimate transverse strength in kilograms . . . . .	325.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5874.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1475.
(Sargent)	

The Coast Range of California, most abundant and attaining its greatest development in the San Jacinto Mountains (Sargent).

## 28. *P. tuberculata*, Gord.

### *Knob-Cone Pine*

*Transverse.* Growth rings thick. Summer wood prominent, open, upwards of equal to the spring wood; the tracheids very unequal in regular rows, distinctly rounded, or the outermost more or less compressed and with much thinner walls; the transition from the spring wood gradual. Spring tracheids hexagonal, somewhat variable, in regular rows, the walls thin. Resin passages rather numerous, chiefly in the summer wood, scattering, large; the epithelium in 1-3 rows of large and very thin-walled and resinous cells which form a more or less extended tract and often merge into thicker-walled parenchyma or thin-walled tracheids. Medullary rays rather broad, 1 cell wide, not prominent, sparingly and locally resinous, distant 2-15 rows of tracheids.

*Radial.* Rays sparingly and locally resinous, the resin massive; the ray tracheids about equal to the parenchyma cells, sometimes predominant and interspersed, the upper and lower walls dentate, more or less reticulated throughout. Ray cells of two kinds: (1) thick-walled,



somewhat fusiform cells chiefly confined to the low rays and somewhat rare; the terminal walls thin and locally thickened; the upper and lower walls thick and strongly pitted; the lateral walls with round or lenticular and usually simple, rarely bordered pits, 2-4 per tracheid; and (2) fusiform cells, with the terminal, upper, and lower walls very thin and usually much broken out; the lateral walls with variously lenticular, round or oval pits, 2-4, chiefly 4, per tracheid, in the summer wood reduced to 2, and finally to 1, and becoming very narrow and much-prolonged slits. Bordered pits in 1 row, sometimes in pairs, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not numerous, medium to low, narrow, very unsymmetrical, the terminals chiefly acute, rarely somewhat prolonged; the inflated portion wholly composed of very thin-walled cells which are commonly broken out. Ordinary rays medium, rather numerous and very broad, presenting three principal aspects: (1) low rays wholly composed of terminal tracheids and thin-walled, resinous parenchyma commonly broken out; (2) higher rays composed of very thin-walled, resinous parenchyma much broken out, with terminal, interspersed and predominant, small tracheids which cause local contraction; and (3) low rays composed of tracheids with 1 central, thick-walled parenchyma cell.

A tree 18-22 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, soft, not strong, brittle, coarse grained, and compact.

Specific gravity . . . . .	0.3499
Percentage of ash residue . . . . .	0.33
Approximate relative fuel value . . . . .	34.88
Coefficient of elasticity in kilograms on millimeters . . . . .	429.
Ultimate transverse strength in kilograms . . . . .	175.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4207.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1372.
(Sargent)	

Dry, gravelly ridges and slopes, not common, 2500-5000 feet elevation. Valley of the Mackenzie River, Oregon, and southward along the slopes of the Cascade and Sierra Nevada mountains, and in the California Coast Range from Santa Cruz to the San Jacinto Mountains (Sargent).

## 29. *P. Torreyana*, Torr.

### *Soledad Pine*

*Transverse.* Growth rings variable, the structure showing a marked tendency to radial fracture. Summer wood prominent but rather open, about one third the spring wood, from which the transition is abrupt when thin, but when thicker the transition is often gradual both ways; the tracheids large, squarish, and often in irregular rows. Spring tracheids large, squarish, rather uniform in regular rows, the walls medium. Resin passages scattering, medium; the epithelium composed of large, thin-walled, irregular and resinous cells in 1-3 rows,

which form an irregular tract and outwardly pass into occasional thick-walled cells. Medullary rays broad, 1 cell wide, not very prominent, distant 2-10 rows of tracheids.

*Radial.* Rays sparingly resinous, the resin confined to the thin walls; the tracheids about equal to, or in the low rays exceeding, the parenchyma cells; rarely interspersed, strongly reticulated throughout. Ray cells of two kinds: (1) cells rather abundant, chiefly straight; the terminal walls thin and entire; the upper and lower walls thick, coarsely and imperfectly pitted; the lateral walls with very prominent and round, elliptical or oblong pits which sometimes become distinctly bordered in the summer wood, 2-4, chiefly 4, per tracheid; and (2) cells broad, fusiform, and variable; the terminal, upper, and lower walls very thin and much broken down; the lateral walls with oval or lenticular variable pits which become very narrow and often much elongated in the summer wood, 2-3 per tracheid. Bordered pits in 1 row, sometimes in pairs, elliptical, in the summer wood quickly reduced to 12-14  $\mu$ , and finally to 7.2  $\mu$ . Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, small to medium, the terminals acute, rarely somewhat prolonged, usually inflated for the whole height; the cells of the terminals composed of thick-walled parenchyma and small tracheids, those of the inflated portion very thin-walled and generally broken out. Ordinary rays low to medium, somewhat numerous, broad, very rarely contracted by the small and much narrower, interspersed tracheids of the highest rays; thick-walled parenchyma cells few; thin-walled parenchyma cells predominant, resinous, much broken out.

A low, short-lived, gnarled, and crooked tree 6-8 m. high, with a trunk upwards of .33 m. in diameter.

Wood light, soft, not strong, brittle, rather close grained, and compact.

Specific gravity . . . . .	0.4879
Percentage of ash residue . . . . .	0.35
Approximate relative fuel value . . . . .	50.62
Coefficient of elasticity in kilograms on millimeters . . . . .	542.
Ultimate transverse strength in kilograms . . . . .	323.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	4548.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2309.
(Sargent)	

A very local tree in San Diego County, California, and possibly Lower California and the islands off Santa Barbara (Sargent).

### 30. *P. chihuahuana*, Engelm.

#### *Yellow Pine*

*Transverse.* Growth rings thin, variable. Summer wood thin, variable, the thicker zones dense, the thin zones open; the transition from the spring wood rather abrupt; the tracheids in regular rows, variable. Spring tracheids squarish-hexagonal, very unequal in regular rows,

the walls rather thin. Resin passages very round, large, somewhat numerous; the epithelium cells at first flattened and rather thin-walled, quickly passing into large, rounded, thick-walled, and strongly resinous wood-parenchyma cells which often form extensive and somewhat irregular tracts. Medullary rays prominent, resinous, broad, 1 cell wide, distant 2-10 rows of tracheids.

*Radial.* Rays locally and strongly resinous, the resin massive; the ray tracheids low, marginal, and interspersed, often predominant, strongly dentate and sparingly reticulated in the summer wood. Ray cells of two kinds, but merging and not always clearly distinguishable: (1) thick-walled, fusiform cells; the terminal walls thin and locally thickened; the upper and lower walls coarsely pitted; the lateral walls with very variable, oval, or lenticular pits, 2-4, chiefly 3, per tracheid, becoming 1 in the summer wood; and (2) thin-walled, fusiform cells; the terminal, upper, and lower walls thin and not pitted, the former often locally thickened; the lateral walls with lenticular, chiefly narrow and simple pits, 2-4 per tracheid, becoming 1-2 in the summer wood. Bordered pits in 1 row, sometimes in pairs, elliptical, becoming smaller toward the summer wood, where they are finally obscure. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, low, variable, rather broad and unsymmetrical; the terminals acute or prolonged; the cells variable, chiefly thick-walled throughout, often resinous. Ordinary rays low, numerous, resinous, and strongly contracted by the frequently interspersed and much narrower tracheids; the parenchyma cells of two kinds: (1) thick-walled cells chiefly predominant; and (2) thin-walled cells more or less broken out, interspersed.

A small tree 18-24 m. high, with a trunk upwards of .45-.60 m. in diameter. Wood light, soft, strong, brittle, close grained, and compact.

Specific gravity . . . . .	0.5457
Percentage of ash residue . . . . .	0.39
Approximate relative fuel value . . . . .	54.37
Coefficient of elasticity in kilograms on millimeters . . . . .	726.
Ultimate transverse strength in kilograms . . . . .	355.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5398.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2470.
(Sargent)	

Dry, rocky ridges and slopes between 5000 and 7000 feet elevation. Arizona, New Mexico, and Chihuahua, Mexico, not common (Sargent).

### 31. *P. Jeffreyi*, A. Murr.

#### *Bull Pine. Black Pine*

*Transverse.* Growth rings narrow, rather uniform. Summer wood thin and open, or again very thin and very open; the tracheids uniform in regular rows, more rarely unequal in irregular rows; the transition from the spring wood rather gradual. Spring tracheids large, hexagonal,

very unequal in regular rows, the walls rather thin. Resin passages large, scattering; the epithelium composed of very large, rounded, rather thin-walled and variable cells in 1-3 rows, often forming rather large tracts. Medullary rays broad, 1 cell wide, not very prominent, distant 2-16 rows of tracheids.

*Radial.* Rays nonresinous; the tracheids strongly dentate and more or less reticulated throughout, numerous and strongly predominant. Ray cells of two kinds: (1) thick-walled cells prominent, fusiform, equal to about 5 spring tracheids; the terminal walls locally thickened; the upper and lower walls strongly thickened and pitted; the lateral walls with prominent, round pits, 2-5, chiefly 3-4, per tracheid, continuous with and merging into the cells of the second order; and (2) fusiform cells equal to about 5 spring tracheids; the terminal walls thin and not locally thickened; the upper and lower walls thin and entire or more rarely locally thickened; the lateral walls with lenticular or oval, very variable pits, 1-4 per tracheid. Bordered pits in 1 row, sometimes in pairs, elliptical, becoming quickly reduced in the summer wood, and finally  $7.2\ \mu$ . Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays few, medium, the terminals acute or somewhat prolonged; the cells of the inflated portion large and thin-walled, usually much broken out. Ordinary rays rather numerous, medium to high, nonresinous, chiefly composed of narrow tracheids with interspersed and much broader parenchyma cells. Parenchyma cells of two kinds: (1) thick-walled cells which predominate in low rays, becoming interspersed in high rays; and (2) the usually broader, more squarish, and thin-walled cells.

A large tree 30-31 m. high, with a trunk upwards of 4 m. in diameter.

Wood light, strong, hard, rather coarse grained, and compact.

Specific gravity . . . . .	0.5206
Percentage of ash residue . . . . .	0.26
Approximate relative fuel value . . . . .	50.53
Coefficient of elasticity in kilograms on millimeters . . . . .	925.
Ultimate transverse strength in kilograms . . . . .	318.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6679.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1850.
(Sargent)	

Dry, gravelly slopes between 6000 and 8000 feet elevation. Along the Sierra Nevadas of California from Siskiyou Mountains to the San Bernardino and San Jacinto mountains (Sargent).

### 32. *P. ponderosa*, Lawson

*Yellow Pine. Bull Pine*

*Transverse.* Growth rings thin, variable. Summer wood variable, dense, sometimes open, the transition from the spring wood often abrupt; the tracheids round-hexagonal, unequal, and in somewhat irregular rows.

Spring tracheids squarish-hexagonal, variable, in somewhat regular rows, rather thick-walled. Resin passages medium, numerous, chiefly in the summer wood; the epithelium in 1-3 rows of rather large and very thin-walled cells, succeeded by thick-walled elements, the whole forming a somewhat extended tract which commonly breaks out in making transverse sections. Medullary rays very broad, 1 cell wide, nonresinous, not numerous, distant 2-15, or sometimes 20 rows of tracheids.

*Radial.* Rays nonresinous; the tracheids predominant or equal to the parenchyma cells, and usually strongly reticulated. Parenchyma cells of two kinds: (1) rather few; the terminal walls thin and locally thickened; the upper and lower walls rather thick but not very strongly pitted; the lateral walls with very conspicuous, round or lenticular, very variable pits, 2-4, rarely 5, per tracheid; and (2) variously contracted cells, the terminal, upper, and lower walls thin and entire; the lateral walls with lenticular or oval pits, 1-4 per tracheid. Bordered pits in 1 row, round or more generally elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays somewhat numerous, low to medium; the terminals acute, composed wholly of tracheids; the cells of the inflated portion very thin-walled and usually broken out. Ordinary rays low, numerous, nonresinous; the tracheids chiefly terminal or when interspersed causing a slight contraction; the thick-walled parenchyma cells chiefly terminal, few, the thin-walled parenchyma occupying the central region and forming the greater portion of the ray, generally broken out, the cells oval, variable.

A large tree 61-91 m. in height, with a trunk upwards of 4.57 m. in diameter.

Wood varying greatly in quality and value, heavy, hard, strong, brittle, not coarse grained or durable, compact.

Specific gravity . . . . .	0.4715
Percentage of ash residue . . . . .	0.35
Approximate relative fuel value . . . . .	46.99
Coefficient of elasticity in kilograms on millimeters . . . . .	887.
Ultimate transverse strength in kilograms . . . . .	307.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6037.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1719.

(Sargent)

Interior of British Columbia south of latitude 51°, south and east along the mountains of the Pacific region to Mexico, the Black Hills of Dakota, Colorado, and western Texas. Dry, rocky ridges; rarely in cold, wet swamps, reaching its greatest development on the western slope of the California Sierras. After *Pseudotsuga Douglasii*, the most generally distributed and most valuable timber tree of the Pacific forests (Sargent). The distribution of this species and the qualities of the wood are not clearly separable from the next species.

**33. *P. scopulorum*, Lemmon**

*Transverse.* Summer wood very variable, rather open, commonly double; the tracheids in very regular rows and uniform, but generally much compressed; the transition from the spring wood rather abrupt. Spring tracheids conspicuously squarish, rather uniform in regular rows, large and thin-walled. Resin passages rather numerous and scattering, not large; the epithelium nonresinous, composed of about 2 rows of very large and very thin-walled cells, those of the limiting layer flattened, those of the secondary layers round, merging into a few thick-walled, round parenchyma cells on the borders of the wood tracheids. Medullary rays rather broad, 1 cell wide, rather numerous but not prominent, distant 2-10, more rarely 17, rows of tracheids.

*Radial.* Rays nonresinous; the ray tracheids commonly high, marginal, or becoming interspersed in the higher rays, predominant and sparingly reticulated. Ray cells of two kinds: (1) the terminal walls thin and locally thickened; the upper and lower walls thick and strongly pitted; the lateral walls with round, simple pits 1-4 per tracheid, conterminous and interspersed with those of the second order; and (2) the terminal, upper, and lower walls thin and not pitted or locally thickened; the lateral walls with small, lenticular pits, 2-4, chiefly 4, per tracheid, becoming 1 or 2 in the summer wood. Bordered pits in 1 row, numerous, crowded, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not numerous, narrow; the somewhat prolonged terminals composed of tracheids; the inflated portion composed of very thin-walled cells, usually all broken out. Ordinary rays rather numerous, low to medium, nonresinous, conspicuously contracted by the somewhat narrower, sometimes interspersed, and conspicuously predominant tracheids; the thick-walled parenchyma cells few, not prominent, the thin-walled parenchyma cells occupying the central tract, oval, variable.

**34. *P. pungens*, Michx. f.**

*Table Mountain Pine. Hickory Pine*

*Transverse.* Growth rings thick. Summer wood very prominent, dense or sometimes somewhat open, often double, the transition from the spring wood gradual, sometimes abrupt; the tracheids in regular rows, variable, rounded. Spring tracheids strongly hexagonal, very unequal in regular rows, the walls rather thick. Resin passages rather large, numerous, chiefly in the summer wood; the epithelium in 1 row of very thin-walled and nonresinous cells, rarely much exceeding the canal and forming eccentric tracts of limited extent. Medullary rays rather broad, somewhat prominent, numerous, distant 2-15 rows of tracheids.

*Radial.* Rays somewhat resinous throughout; the tracheids variable, often predominant, reticulated throughout and more or less interspersed. Ray cells of two kinds: (1) cells numerous and long fusiform; the terminal walls entire or locally thickened; the upper and lower walls strongly thickened and coarsely pitted; the lateral walls with very variable, oval, or lenticular pits, 1-3 per tracheid, in the summer wood distinctly bordered, the orifice a prolonged slit; and (2) cells variously

fusiform, the terminal, upper, and lower walls thin and usually much broken out; the lateral walls with lenticular or oval, very variable pits, 1-4, chiefly 2 or 3, per tracheid, in the summer wood becoming distinctly bordered, the orifice an extended slit, conterminous with tracheids and cells of the first order. Bordered pits in 1 row or pairs, elliptical, and toward the summer wood soon replaced by narrow slits, which often lead into strong, double striations. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays not numerous, low and broad, the chiefly acute terminals composed of a few tracheids; the cells of the inflated portion very thin-walled, chiefly broken out, or again rather thick-walled in part and persistent. Ordinary rays low to medium and presenting four principal aspects: (1) low rays of thin-walled parenchyma, much broken out, and small, terminal tracheids; (2) low rays of thick-walled parenchyma and small, terminal tracheids; (3) higher rays of thick-walled parenchyma and both terminal and interspersed tracheids with occasional thin-walled parenchyma; and (4) the highest rays of thin-walled, resinous, and interspersed thick-walled parenchyma, together with terminal and interspersed tracheids.

A tree 9-18 m. high, with a trunk upwards of 1.05 m. in diameter. Wood light, soft, not strong, brittle, coarse grained, and compact.

Specific gravity . . . . .	0.4935
Percentage of ash residue . . . . .	0.27
Approximate relative fuel value . . . . .	49.22
Coefficient of elasticity in kilograms on millimeters . . . . .	803.
Ultimate transverse strength in kilograms . . . . .	310.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5670.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1842.
(Sargent)	

Allegheny Mountains, Pennsylvania to Tennessee, in the high mountains of the latter attaining its greatest development (Sargent).

### 35. *P. inops*, Ait.

#### *Jersey Pine. Scrub Pine*

*Transverse.* Growth rings thick, often double. Summer wood rather dense, sometimes more or less open, equal to about one fourth or one third the spring wood, from which the transition is usually abrupt; the tracheids strongly unequal, chiefly in regular rows. Spring tracheids squarish, large, very uniform in regular rows, the walls thin. Resin passages rather numerous, medium; the epithelium in 1-2 rows of large, round, thin-walled or again rather thick-walled, resinous cells, which are often developed eccentrically about the canal, and become thicker-walled especially on the outer limits. Medullary rays prominent, rather broad, 1 cell wide, not numerous, distant 2-12 rows of tracheids.

*Radial.* Rays somewhat resinous, the resin massive, localized; the tracheids numerous, low, very variable and very strongly reticulated throughout, predominant, often interspersed. Ray cells of two kinds: (1) the terminal

walls thin and locally thickened; the upper and lower walls more or less thickened and coarsely pitted; the lateral walls with lenticular or oval, variable pits, 2-6, chiefly 4, per tracheid, finally becoming slit-like and reduced to 1 in the summer wood or eventually obsolete, often conterminous with tracheids or with thin-walled parenchyma cells; and (2) the predominant elements; the terminal, upper, and lower walls thin; the lateral walls with very variable, oval, or lenticular pits, 1-4 or more rarely 5, chiefly 4, per tracheid, in the summer wood merging into prolonged slits or finally into round, bordered pits with an oblong, narrow orifice; fusiform, chiefly high. Bordered pits in 1 row or pairs, elliptical, becoming round and conspicuously smaller toward the summer wood, where they are finally reduced to  $7.2 \mu$ . Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays medium, rather few, narrow; the terminals acute and composed of large and small tracheids; the inflated portion composed of thin-walled tissue, much broken out and more or less resinous. Ordinary rays chiefly low and presenting three principal aspects: (1) low rays distinctly fusiform, with a large tracheid in the center and small terminal tracheids; (2) higher rays of 1-several large, thin-walled, and resinous cells, much broken out, with or without interspersed thick-walled cells, sometimes in pairs, and terminal tracheids of variable size; and (3) the highest rays composed of large, thin-walled parenchyma cells, often with resin, but usually much broken out, terminal tracheids and 1-several small, interspersed tracheids, causing local contractions.

A tree 24-36 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, soft, not strong, brittle, very close grained, compact, and durable.

Specific gravity . . . . .	0.5309
Percentage of ash residue . . . . .	0.30
Approximate relative fuel value . . . . .	52.93
Coefficient of elasticity in kilograms on millimeters . . . . .	543.
Ultimate transverse strength in kilograms . . . . .	281.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5765.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2496.
(Sargent)	

Sandy, generally barren soil. Long and Staten islands, New York; southward usually near the coast to South Carolina and westward through eastern and middle Kentucky to southeastern Indiana (Sargent).

### 36. *P. muricata*, D. Don

#### *Prickle-Cone Pine*

*Transverse.* Growth rings thick. Summer wood prominent but rather thin, about one fifth the spring wood, variable, both dense and open; the tracheids variable, in the open zones often much compressed and in irregular rows, the walls variable; the transition from the spring wood rather gradual. Spring tracheids hexagonal, unequal, in regular rows,



the walls rather thin. Resin passages scattering, rather small, somewhat numerous, chiefly in the summer wood; the epithelium in 1-2 rows of large, rounded, thin-walled, often strongly resinous cells, which sometimes become thick-walled at the outer limits. Medullary rays not numerous or prominent, rather narrow, 1 cell wide, distant 2-30 rows of tracheids.

*Radial.* Rays locally somewhat resinous, the resin massive; the ray tracheids strongly predominant, often composing the entire structure of the low rays, in the higher rays marginal, more rarely interspersed, reticulated in the summer wood. Ray cells of two kinds:<sup>1</sup> (1) rather frequent but not predominant except in the low rays, rather high and long fusiform; the terminal walls thin, sometimes strongly pitted; the upper and lower walls rather thick and coarsely pitted; the lateral walls with prominent and very variable, oval, round, or lenticular pits, 1-4 per tracheid; and (2) cells resinous, the terminal, upper, and lower walls thin and much broken out; the lateral walls with lenticular pits 1-3, chiefly 2, per tracheid. Bordered pits in 1 row, sometimes in pairs, numerous, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays low, the terminals acute, rarely prolonged; the cells of the inflated portion large and rather thin-walled, often wholly broken out. Ordinary rays low, rather broad, the cells very variable in shape from oval to squarish, and presenting four principal aspects: (1) low, fusiform in shape, composed of thick-walled, oval parenchyma cells with terminal tracheids; also higher rays of the same aspect; (2) low rays of thick- and thin-walled, oval parenchyma — the latter resinous, but otherwise not very different — and small, terminal tracheids; (3) higher rays of large, broad, thin-walled, resinous parenchyma, 1-2 thick-walled parenchyma cells and terminal tracheids; and (4) the highest rays of thick-walled parenchyma and interspersed tracheids with local contractions. Parenchyma cells oval, very narrow.

A tree 24-36 m. high, with a trunk upwards of .90 m. in diameter.

Wood light, very strong and hard, coarse grained, and compact.

Specific gravity . . . . .	0.4942
Percentage of ash residue . . . . .	0.26
Approximate relative fuel value . . . . .	49.29
Coefficient of elasticity in kilograms on millimeters . . . . .	1194.
Ultimate transverse strength in kilograms . . . . .	441.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	8142.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1950.
(Sargent)	

The coast ranges of California, reaching its greatest development in Mendocino County. Rare and local, in cold peat bogs or barren, sandy gravel below 2000 feet elevation (Sargent).

<sup>1</sup> The distinction between these two forms of cells is not very clear in this species and is best expressed by the terms "thicker" and "thinner" as applicable to elements which are not *very* different, or which merge by gradual transitions.

37. *P. insignis*, Douglas*Monterey Pine*

*Transverse.* Growth rings thick, often double. Summer wood rather open, the transition from the spring wood very gradual; the tracheids very unequal in more or less irregular rows, often strongly compressed radially. Spring tracheids hexagonal, very unequal in somewhat regular rows, the walls medium. Resin passages scattering, numerous, rather large; the epithelium in 1-3 rows of very large, round, but variable and rather thin-walled, resinous cells. Medullary rays very prominent, broad, 1 cell wide, not very numerous, distant 2-12, more rarely 21, rows of tracheids.

*Radial.* Rays resinous, the resin localized, granular, more rarely massive or in the cell wall; the ray tracheids sparingly reticulated and sparingly predominant, when interspersed, very low and unequal. Ray cells of two kinds: (1) cells usually low and prominent, especially in the low rays; the terminal walls often thick and coarsely pitted; the upper and lower walls very variable, in the low rays thick and coarsely pitted, in the higher rays thin and barely pitted so as to approach cells of the second order; the lateral walls with variously oval or lenticular pits, 1-2, rarely 6, chiefly 2, per tracheid; (2) cells straight or variously fusiform; the terminal, upper, and lower walls very thin, commonly much broken out; the lateral walls with broadly oval or variously lenticular pits, 1-3 per tracheid, in the summer wood reduced to much-prolonged slits. Bordered pits in 1 row, sometimes in pairs, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays somewhat abundant, medium, rather narrow, the terminals acute or somewhat prolonged, chiefly composed of small tracheids; the cells of the inflated portion chiefly thin-walled and usually much broken out, but dark and resinous. Ordinary rays medium, rather broad, composed of thicker- and thinner-walled cells and presenting four principal aspects: (1) low rays composed of thick-walled parenchyma and tracheids, distinctly fusiform; (2) 1-seriate rays composed of several cells of thick-walled parenchyma and tracheids, usually nonresinous; (3) 1-seriate rays composed of terminal tracheids, thick-walled and thin-walled parenchyma, usually much broken out through the central region, more or less resinous; and (4) the highest rays showing interspersed, narrow tracheids with strong, local contractions.

A tree 24-30 m. high, with a trunk upwards of .90 in diameter.

Wood light, soft, not strong, brittle, close grained, and compact.

Specific gravity . . . . .	0.4574
Percentage of ash residue . . . . .	0.30
Approximate relative fuel value . . . . .	45.60
Coefficient of elasticity in kilograms on millimeters . . . . .	979.
Ultimate transverse strength in kilograms . . . . .	316.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6680.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1687.
(Sargent)	

Rare and local, on sandy soil in proximity to the seacoast, California (Sargent).

38. *P. Sabiniana*, Douglas*Digger Pine. Bull Pine*

**Transverse.** Growth rings thick, variable, often double. Summer wood variable, upwards of one fourth to one half the spring wood, from which the transition is somewhat abrupt, dense, or again rather open; the tracheids very unequal, chiefly in irregular rows, the larger ones often much compressed. Spring tracheids rather large, squarish-hexagonal, uniform in regular rows, the walls thickish. Resin passages medium, not very numerous, chiefly in the summer wood; the epithelium of 2 or more rows of large, irregularly flattened and very thin-walled, somewhat resinous cells, often forming an irregular and somewhat extended tract. Medullary rays prominent, somewhat resinous, broad, 1 cell wide, distant 2-10 rows of tracheids.

**Radial.** Rays sparingly resinous; the tracheids low but very variable, marginal, predominant and sparingly interspersed, often composing the entire structure of low rays, strongly dentate and somewhat reticulate in the summer wood. Ray cells of two kinds: (1) cells rather numerous, chiefly in low rays; the upper and lower walls thick, strongly but irregularly pitted; the lateral walls with prominent, round and bordered, or simple and lenticular pits, 2-5, chiefly 4, per tracheid; (2) cells rather low and variable, not conspicuously fusiform; the terminal, upper, and lower walls very thin and entire; the lateral walls with variously lenticular pits without an obvious border, 2-4, chiefly 2, per tracheid, becoming reduced to 1 in the summer wood. Bordered pits conspicuously in 1-2 rows, numerous, elliptical, becoming smaller and round toward the summer wood. Pits on the tangential walls of the summer wood wholly wanting.

**Tangential.** Fusiform rays rather numerous, narrow; the terminals acute or prolonged linear, chiefly composed of tracheids; the cells of the inflated portion large and very thin-walled, often much broken out. Ordinary rays chiefly low, not very numerous, nonresinous, broad, the tracheids chiefly terminal and much narrower, rarely interspersed, presenting four principal aspects: (1) thin-walled parenchyma with terminal and interspersed tracheids; (2) 1-seriate rays with a few terminal, thick-walled tracheids, but chiefly composed of large and very thin-walled parenchyma cells; (3) thin-walled parenchyma with terminal tracheids and interspersed, thick-walled parenchyma; and (4) 1-seriate rays composed of tracheids and thick-walled parenchyma.

A large tree 24-30 m. high, with a trunk upwards of 1.20 m. in diameter.

Wood light, soft, not strong, brittle and very coarse grained, compact, not durable.

Specific gravity . . . . .	0.4840
Percentage of ash residue . . . . .	0.40
Approximate relative fuel value . . . . .	48.18
Coefficient of elasticity in kilograms on millimeters . . . . .	585.
Ultimate transverse strength in kilograms . . . . .	333.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	5387.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2202.

(Sargent)

Very common in the foothills region; Coast Range and western slope of the Sierra Nevadas below 4000 feet elevation, California (Sargent).

39. *P. taeda*, Linn.*Loblolly Pine. Old Field Pine*

**Transverse.** Growth rings broad. Summer wood open or sometimes rather dense, often double and often equal to the spring wood, from which the transition is abrupt; the tracheids large, strongly unequal but in rather regular rows. Spring tracheids large, squarish, the walls thin. Resin passages numerous, chiefly in the summer wood, very large; the epithelium composed of very thin-walled, sometimes resinous cells, chiefly in 1 row and strongly compressed upon the face of the tracheid structure, more rarely becoming 2-rowed in part and forming an eccentric tract of limited extent. Medullary rays rather prominent, broad, 1 cell wide, distant 2-8 rows of tracheids.

**Radial.** Rays nonresinous; the tracheids sometimes predominant in the higher rays, but often interspersed, low and unequal throughout, sparingly, rarely strongly reticulated. Ray cells of two kinds: (1) cells rare and occurring only (?) in the low rays, where they are continuous with the tracheids; the terminal walls thin and entire; the upper and lower walls thick and strongly but incompletely pitted; the lateral walls with round or oval pits, upwards of 6 per tracheid; (2) cells variously fusiform, often straight; the terminal, upper, and lower walls very thin and commonly much broken out; the lateral walls with variable, oval, or lenticular pits, 1-6, chiefly 2-4, per tracheid, in the summer wood commonly reduced to 1. Bordered pits in 1 or 2 rows or often 1 row or pairs, elliptical. Pits on the tangential walls of the summer wood wholly wanting. The tracheids of the summer wood sometimes exhibit a distinct tendency toward the formation of spirals.

**Tangential.** Fusiform rays rather high and narrow, the terminals acute or prolonged and finally wholly composed of small tracheids; the cells of the inflated portion commonly wanting. Ordinary rays medium and presenting two principal aspects: (1) higher rays composed of thin-walled parenchyma cells chiefly broken out, with very small, terminal, and interspersed tracheids, the latter causing local contractions; and (2) lower rays of thin-walled parenchyma much broken out, rarely showing a thick-walled parenchyma cell, and small, terminal tracheids.

A large tree 24-46 m. high, with a trunk upwards of 1.50 m. in diameter.

Wood light, not strong, brittle and very coarse grained, not durable.

Specific gravity . . . . .	0.5441
Percentage of ash residue . . . . .	0.26
Approximate relative fuel value . . . . .	54.27
Coefficient of elasticity in kilograms on millimeters . . . . .	1128.
Ultimate transverse strength in kilograms . . . . .	377.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	6834.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	1719.

(Sargent)

Low, wet clay or sandy soil; southern Delaware to Tampa Bay, Florida, generally near the coast; westward through the Gulf States to the valley of the Colorado River, Texas, and northward through southern Arkansas to the valley of the Arkansas River (Sargent).

40. *P. palustris*, Miller*Long-Leaved Pine. Southern Pine. Yellow Pine*

**Transverse.** Growth rings thin, very variable. Summer wood dense, often very thin, the transition from the spring wood very abrupt; the tracheids very uniform in regular rows. Spring tracheids squarish, rather uniform, in regular rows, often radially elongated, the walls rather thick. Resin passages numerous and large, chiefly in the summer wood; the epithelium composed of large, rounded, often resinous cells in 1 row, frequently becoming several-rowed in part and forming more or less extensive and strongly eccentric tracts about the canal. Medullary rays very prominent, broad, 1 cell wide, distant 2-10, more rarely 15, rows of tracheids.

**Radial.** Rays sparingly resinous throughout; the ray tracheids often interspersed, commonly predominant, very strongly reticulated throughout. Ray cells of two kinds: (1) rather few but prominent and conterminous with tracheids into which they merge; the terminal walls thin and not pitted; the upper and lower walls somewhat strongly but unequally thickened and pitted; the lateral walls with broadly and variously lenticular or round pits, 2-5 per tracheid; and (2) very long-fusiform cells; the terminal, upper, and lower walls very thin and usually much broken out; the lateral walls with very variable, lenticular, or oval, sometimes very large, pits, 2-6, chiefly about 4, per tracheid, in the summer wood reduced to 1. Bordered pits conspicuously in 1-2 rows, elliptical. Pits on the tangential walls of the summer wood wholly wanting.

**Tangential.** Fusiform rays not numerous, often very high, acute, the linear terminals much prolonged with terminal or interspersed tracheids, but with the structure very commonly wanting except at the extremities; the low, inflated portion usually showing only a remnant of very thin-walled, delicate tissue. Ordinary rays medium, rather numerous, broad, presenting three principal aspects: (1) low rays with few, thin-walled parenchyma cells much broken out, and terminal tracheids of very variable size; (2) higher rays of several large, thin-walled parenchyma cells much broken out, and narrow, oval to oblong, terminal tracheids, rarely with interspersed thick-walled parenchyma; and (3) the highest rays composed of a few large, thin-walled parenchyma cells, with small, terminal, and narrow, often high and interspersed tracheids.

A tree of the greatest economic value 18-29 m. high, with a trunk upwards of 1.20 m. in diameter.

Wood heavy, exceedingly hard, very strong and tough, coarse grained, compact, and durable.

Specific gravity . . . . .	0.6999
Percentage of ash residue . . . . .	0.25
Approximate relative fuel value . . . . .	69.82
Coefficient of elasticity in kilograms on millimeters . . . . .	1,488.
Ultimate transverse strength in kilograms . . . . .	490.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	10,074.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2,508.
(Sargent)	

Dry, sandy loam of the coastal plain, forming extensive forests almost to the exclusion of other species; rarely found along the borders of swamps in low, wet soil. Southeastern Virginia to Tampa Bay, Florida; westward through the Gulf States to the Red River in Louisiana, and the Trinity River in Texas; rarely more than 150 miles from the coast (Sargent).

#### 41. *P. cubensis*, Griseb.

*Slash Pine. Swamp Pine*

*Transverse.* Growth rings variable. Summer wood variable, dense or open, the transition from the spring wood usually *very* abrupt; the tracheids conspicuously rectangular, very uniform and regular, with small, round cavities and very thick walls, or again strongly rounded, very unequal, often much compressed, the general structure both open and dense. Spring tracheids squarish or rounded, the walls rather thin. Resin passages numerous, large, chiefly in the summer wood; the epithelium in 1-2, rarely 3, rows of rather thin-walled, usually much flattened, resinous cells. Medullary rays prominent, very broad, 1 cell wide, numerous, distant 2-8, rarely 12, rows of tracheids.

*Radial.* Rays sparingly resinous; the ray tracheids rather high, predominant in the low rays, everywhere very strongly reticulated. Ray cells of two kinds: (1) short-fusiform cells equal to about 4 spring tracheids; the terminal walls thin and entire, locally thickened or coarsely pitted; the upper and lower walls thin and much broken down, but more commonly thicker and irregularly pitted, these two forms gradually merging so that they are not readily separable, sometimes conterminous with and merging into tracheids; the lateral walls with variable, chiefly lenticular pits, 1-6, chiefly about 2-4, per tracheid, in the summer wood reduced to slits or becoming obsolete. Bordered pits in 1-2 rows, numerous, elliptical, in the summer wood quickly reduced and finally obscure or wholly wanting. Pits on the tangential walls of the summer wood wholly wanting.

*Tangential.* Fusiform rays rather numerous, high, and narrow, the terminals acute or prolonged and composed of very large, broadly oval parenchyma cells and very large, terminal tracheids; the short, inflated portion composed of thin-walled parenchyma cells much broken out. Ordinary rays rather numerous, broad, medium, the cells chiefly broadly oval; composed of dominant parenchyma cells with chiefly terminal, sparingly interspersed, often high, and narrow tracheids.

A tree 24-30 m. high, with a trunk upwards of .90 m. in diameter.

Wood heavy, exceedingly hard, very strong, tough, coarse grained, compact, and durable.

Specific gravity . . . . .	0.7504
Percentage of ash residue . . . . .	0.26
Approximate relative fuel value . . . . .	74.83
Coefficient of elasticity in kilograms on millimeters . . . . .	1,577.
Ultimate transverse strength in kilograms . . . . .	500.
Ultimate resistance to longitudinal crushing in kilograms . . . . .	10,626.
Resistance to indentation to 1.27 mm. in kilograms . . . . .	2,985.
(Sargent)	

South Carolina and southward near the coast to the Florida Keys; westward along the Gulf coast to the Pearl River, Louisiana, not more than 50 or 60 miles inland; also in the West Indies (Sargent); Bahamas and Isle of Pines (Shaw).

#### B. PITYOXYLON (Pinoxylon)

##### *Fossil Species Only*

#### 42. *P. dacotense*, Knowlton

"*Transverse*. Annual rings broad and very distinct, even to the naked eye, being 2-4.5 mm. in width. Distinction between the spring and autumn wood very plain, the former appearing as broad, white bands, and the latter as dense black bands of varying width. Under the microscope the line of demarcation between fall and spring wood is observed to be very sharp indeed. The fall wood consists of thick-walled cells of an elliptical or oblong outline, rather loosely placed. The succeeding spring wood is composed of very large cells with relatively thin walls. The medullary rays are long and quite thick-walled. There are no resin cells in the wood. The resin passages are present and quite numerous. They do not seem to be confined to any particular portion of the ring, but are scattered, being perhaps most numerous in the fall wood. They are of relatively large size and lined with thin-walled epithelium.

"*Radial*. The walls of the spring and summer wood have 2 rather irregular rows of large, bordered pits. In rare cases these pits are in a single row. The average size of the outer circle is .025 mm., that of the inner circle about .015 mm. The cells of the rays are rather long, covering the width usually of some 4 or more cells of the spring wood. They are rather thick-walled, the walls being strongly dentate or somewhat irregularly thickened. The ray cells are provided with a few scattered, bordered pits, usually only 1 to the width of a spring cell of the wood, although not rarely there are 2 in a similar width. They are always in 1 row on the ray cell.

"*Tangential*. Medullary rays in a single, superimposed series, from 1 to rarely 30 cells, the average being from 5 to 12 cells high. None of the rays in the sections examined are of the fusiform type or contain resin passages. The wood cells are, as far as can be made out, without pits or markings of any kind" (Knowlton).

Trunks of medium size; material silicified.

Upper (?) Jurassic near Sturgis, South Dakota (Knowlton).

#### 43. *P. Aldersoni*, Knowlton

"*Transverse*. The annual rings are very distinct, being plainly discernible to the naked eye. Some of the broadest rings are fully 9 mm. wide and none less than 6 mm. The demarcation between fall and spring wood is very pronounced, the cells of the fall wood being small, compressed, and thick-walled, while those of the early spring wood are very large, and, of course, thin-walled. The cells of the spring and summer wood continue for a width of 5 mm., but little, if any, diminished in size.

Then they become slightly smaller and thicker-walled and pass gradually into the fall wood. The resin ducts are very large. They are not found in the summer wood, but occur irregularly in the early fall and late fall wood. The medullary rays as observed in this section are straight and separated by 3-8 or 10 rows of wood cells. The individual cells are apparently long.

*"Radial.* Notwithstanding the fact that the wood seems to be perfectly preserved, it does not reveal the structure well in this section. The wood cells are seen to be sharp-pointed where they join. They are, of course, broad in the spring and summer wood and very narrow in the fall wood. It is very difficult to make out the pits, but in exceptionally well-preserved portions a few may be faintly seen. They are scattered, but in a single series. They are so obscure that no satisfactory measurements can be made. The medullary rays in this section are long, thick-walled, and without markings, so far as can be made out.

*"Tangential.* This section is very plain. The medullary rays are numerous and in a single series, although occasionally a ray may be observed in which there are 2 series of cells for a short distance. In such cases the cells are always smaller than the ordinary ray cells. The number of cells making up each ray ranges from 2 to 30 or more, but the average number is about 8-15. The rays in which there is a resin duct are rather rare. The duct is large, taking up all the width of the ray. The remainder of the ray is 3 rows of cells high in the middle, and is reduced to 1 at the extremities. The wood cells show plainly in this section. They are not provided with pits or other markings" (Knowlton).

Trunks of large size, 3-5 feet in diameter. Material silicified.

Tertiary of the Yellowstone National Park, at Specimen Ridge, near head of Crystal Creek, and Yancy Fossil Forest (Knowlton).

#### 44. *P. amethystinum*, Knowlton

*"Transverse.* Much like *P. Aldersoni* except that the rings are narrower, the cells of the spring and summer wood are smaller, and the late fall cells have thinner walls. The resin ducts are also much the same, being in general only a little smaller. A few are found in the summer wood, but most of them are in the fall wood. The rays are not nearly so numerous as in the last species. They are often separated by as many as 25 rows of wood cells.

*"Radial.* The radial section of nearly all woods from the Yellowstone National Park is more or less obscure. The one under consideration is no exception to this rule, and it is only after considerable search that the pits can be determined. They are in a single row and are rather small. They are so obscure that it is impossible to make trustworthy measurements. The medullary rays, as seen in this section, are composed of long, thin-walled cells, and, so far as can be determined, they are without pits or other markings.

*"Tangential.* This section shows the structure very plainly. The medullary rays are abundant and always in a single series, except the large, compound ones. The number of cells in each ray varies from 2 to 10 or 12, the average number being about 6. The compound rays inclosing the



resin ducts are rather small, with 3 rows of cells in the middle portion. No markings can be made out on the wood cells in this section" (Knowlton).

This species is very closely allied to the preceding, and should perhaps be referred to it. The main points of difference are the following: smaller resin ducts that are occasionally found in the summer wood; smaller wood cells throughout; smaller and shorter compound medullary rays; ordinary rays always in a single series of 2-12 cells (average 6) instead of 2-30 or more (average 12) (Knowlton).

This species cannot be separated from the preceding on the basis of the characters given, and it is undoubtedly the same, though recognized here provisionally (D.P.P.).

Trunks of small and medium size. Material silicified.

Tertiary of the Yellowstone National Park at Specimen Ridge, near the head of Crystal Creek (Knowlton).

#### 45. *P. columbiana*, Penh.

*Transverse.* Growth rings variable though generally very broad in large stems. Spring wood usually predominant, the transition to the summer wood gradual but in the narrower rings more or less abrupt and sometimes conspicuously so; the tracheids large, thick-walled and often conspicuously so, definitely rounded, often radially oval, chiefly uniform, more or less equal, in regular radial rows. Summer wood conspicuous, dense, and often rather thin. The structure as a whole is that of a rather dense wood of medium hardness. Medullary rays prominent, not very numerous, resinous, and distant upwards of 9 or more rarely 15 rows of tracheids. Resin passages conspicuous, rather large, and scattering throughout the growth ring, the parenchyma cells large, thin-walled, and in 2 rows, or forming large and irregular tracts upwards of 6-9 tracheids wide, resinous; thyloses not obvious.

*Radial.* Medullary rays resinous; the tracheids rather numerous, marginal and interspersed, not obviously predominant, very variable and often as high as or higher than, long, sparingly dentate; the parenchyma cells all of one kind and rather thin-walled, straight, and equal to about 4 wood tracheids; the upper and lower walls strongly (?) pitted; the terminal walls straight or diagonal and apparently not pitted; the lateral walls with simple, round or lenticular pits of medium size, 2-4, chiefly 2, per tracheid. Bordered pits on the tangential walls of the summer tracheids small and not numerous; those of the radial walls rather large, round, or oval in 1 compact row, and generally numerous.

*Tangential.* Fusiform rays rather numerous, short, the broad central tract with thin-walled parenchyma chiefly broken out, the unequal terminals composed of broad, oval cells chiefly in 1 row. Ordinary rays low to medium, 1-seriate, not materially contracted by the interspersed tracheids; the parenchyma cells somewhat unequal and variable from oblong to oval or broad and round.

Calcified fragments of stems and branches, and also cones in the Tertiary of Kettle River, near Midway, British Columbia.

46. *P. Peali*, Knowlton

- "*Transverse*. This section shows the late fall and early spring wood. The contrast in the thickness of the cells makes a very clearly marked ring. This ring of growth was very broad, being in some cases fully 10 mm. The medullary rays show in this section also as long, slender cells.
- "*Radial*. The specimens are in a fine state of preservation. The cells of the spring and summer wood are very broad and marked with a single series of large, scattered, bordered pits. The medullary rays are prominent. They are composed of very long cells, each of which is marked usually by 2 or 3 small, oblong, or nearly circular bordered pits the width of each wood cell.
- "*Tangential*. The medullary rays are arranged in a single series of from 2 to occasionally 20 superimposed cells. The resin tubes occurring in the midst of a medullary ray are quite numerous. There are no recognizable pits or markings on the tangential walls of the wood cells" (Knowlton).

Material silicified.

Miocene of the upper Gallatin Basin, Montana (Knowlton).

47. *P. chasense*, Penh.

- Transverse*. Tracheids chiefly in regular radial rows, very variable in size, squarish, about  $44 \times 44 \mu$  broad; the walls  $12.5 \mu$  thick. Medullary rays numerous, chiefly 1 cell wide, occasionally 2-3 seriate. Growth rings wholly wanting. Resin cells and resin canals not represented.
- Radial*. Ray cells all of one kind; straight, equal to 2-4 tracheids; the upper and lower walls thin and not pitted; the terminal walls thin, not pitted, straight or curved; the structure of the lateral walls not determinable, but the pits are probably round. Bordered pits in 1-3 rows, chiefly 2 rows, round or hexagonal,  $12.5 \mu$  broad, the orifice probably round.
- Tangential*. Rays of two kinds: (1) 1-seriate rays, the cells oblong,  $25 \mu$  broad, often 2-seriate in part; and (2) fusiform rays, the terminals linear and of the structure of the 1-seriate rays; the central tract very broad, nearly round; the cells large, thin-walled, irregular, and inclosing a small, central resin passage with large epithelium cells.

Material silicified. Specimens represented by small fragments of stem.

From the Chase Formation (Permian) at Coon Creek, Chase County, Kansas (Prosser).

48. \* \* *P. statenense*, Jeff. and Chrys.

- Transverse*. Growth rings variable, chiefly narrow but usually well defined; summer wood very variable, of the narrower rings 1-5, but of the broader rings many tracheids thick and constituting upwards of two thirds the total thickness; transition from the spring wood somewhat abrupt; the broader growth rings sometimes showing 2 zones of summer wood. Tracheids round-hexagonal or rectangular, rather

uniform but conspicuously unequal, disposed in unequal and somewhat irregular rows; those of the spring wood thin-walled, about  $32 \times 39 \mu$ , those of the summer wood rather thin-walled, about  $19 \times 29 \mu$ . Medullary rays very resinous, broad, 1 cell wide, and distant about 2-8 rows of tracheids. Specialized resin cells wholly wanting. Resin passages numerous, large, chiefly in the spring wood and filled with prominent, resinous thyloses, the epithelium 1-2 cells thick, and not extended into parenchymatous tracts.

*Radial.* Bordered pits very numerous in 1 row, rarely contiguous; round, more rarely oval, and about  $17.5 \mu$ , the round orifice about  $7 \mu$ ; in the summer wood somewhat reduced. Pits on the tangential walls of the summer wood prominent, large, somewhat numerous. Medullary rays very resinous; ray tracheids wholly wanting; parenchyma cells all of one kind, more or less contracted at the ends, very variable but generally equal to about 3-5 spring tracheids; the upper and lower walls strongly and rather frequently pitted; the terminal walls coarsely pitted or locally thickened; the lateral walls with rather small, oval pits, chiefly 1 per tracheid throughout, or in the marginal cells and low rays 2 per tracheid.

*Tangential.* Fusiform rays numerous, medium; the cells thick-walled; the central tract broad and occupied by 1 large resin canal filled with thyloses; the terminals chiefly short or rarely prolonged with 1-2 seriate cells. Ordinary rays very variable but chiefly low to medium, sometimes more or less 2-seriate in part; very numerous; the cells broad but variable and round, oval or squarish, chiefly equal; in the low rays commonly becoming oblong.

The middle Cretaceous at Kreischerville, Staten Island. Material in the form of lignite (Jeffrey).

#### 49. \* \* *P. scituate* (Jeff. and Chrys).

*Transverse.* Growth rings rather broad but thin, the limits obscured by displacement of structure; summer wood chiefly broad, the transition from the spring wood apparently gradual. Tracheids all rather thin-walled, those of the spring wood about  $26.7 \times 44.5 \mu$ . Medullary rays numerous, prominent, resinous, broad, 1 cell wide and distant about 2-5 rows of tracheids. Resin canals rather numerous, chiefly in the summer wood and central to broad tracts of parenchyma; devoid of thyloses, rather small, regularly oval or round, the epithelium composed of a single layer of rather small, rounded, and somewhat thick-walled cells. Wood parenchyma resinous, the cells large, thin-walled; forming extensive and prominent tracts about the resin canals often  $427 \times 570 \mu$  broad.

*Radial.* Bordered pits in 1 row, somewhat distant and not numerous; round, about  $24.6 \mu$  broad, the lenticular orifice showing a cross; not much reduced in the summer wood. Pits on the tangential walls of the summer tracheids not determinable, apparently wanting. Medullary rays resinous; ray tracheids apparently wanting; the parenchyma cells all of one kind, not contracted at the ends, equal to about 5-8 wood tracheids; the upper and lower walls rather thick, distantly and

coarsely pitted; the terminal walls rather thin and locally thickened; the lateral walls with round, bordered pits about  $11.5\ \mu$  broad, chiefly 1, or sometimes 2, per tracheid, the orifice lenticular, diagonal. Wood parenchyma resinous; the cells cylindrical, 2-several times longer than broad, the radial walls with rather small pits.

*Tangential.* Ordinary rays resinous, numerous, variable, low to high, 1-2 seriate, or sometimes 3-seriate, and approximating to the fusiform type through various gradations, but always devoid of resin canals; the usually large cells very unequal and very variable, ranging from oblong to oval, round or transversely oval, the strong inequality and variability giving a marked irregularity of form to the ray as a whole. Fusiform rays rather numerous, low to high, the central tract occupied by 1 rather small resin canal devoid of thyloses, but with small and thick-walled epithelium cells; the terminals short or sometimes unequally prolonged to considerable length. Wood parenchyma resinous, the short-cylindrical cells with thin walls and bearing pits on all their walls. Rudimentary spirals may be seen in the tertiary layer of many of the tracheid walls.

Cretaceous (?) of Third Cliff, Scituate, Massachusetts. Material in the form of lignite (Bowman).



## APPENDIX A

### DATA FOR TABLE OF ANATOMICAL CHARACTERS, IN IDENTICAL SERIES

1. Spiral tracheids.
  2. Bordered pits in 1-3 rows.
  3. Bordered pits in 1-2 rows.
  4. Bordered pits in 1 row.
  5. Pits on the tangential walls of the summer wood.
  6. Lateral walls of the ray cells with bordered pits.
  7. 1-seriate rays.
  8. Terminal walls of the ray cells thin and entire.
  9. Resin cells.
  10. Terminal walls of the ray cells locally thickened.
  11. Terminal walls of the ray cells strongly pitted.
  12. Ray tracheids.
  13. Resin passages.
  14. Fusiform rays.
  15. Thyloses in the resin passages.
  16. Lateral walls of the ray cells with simple pits.
  17. Ray cells of two kinds.
- 
1. Resin cells scattering.
  2. Resin cells zonate.
  3. Resin cells grouped.
  4. Resin cells on the outer face of the summer wood.
  5. Ray tracheids marginal.
  6. Ray tracheids interspersed.
  7. Ray tracheids dentate.
- 
- A. Number of species.  
B. Percentage value of genus.

APPENDIX A — *Continued*

TABLE OF ANATOMICAL CHARACTERS OF THE CORDAITALES, GINGKOALES, AND CONIFERALES

	A	B
1 Dammara australis . . .	1	16.
2 Araucaria Cunninghamii excelsa . . .	3	17-7
Bidwillii . . .		
3 Ginkgo biloba . . .	1	17-7
4 Torreya taxifolia californica . . .	3	19-0
nucifera . . .		
5 Taxus floridana . . .	4	19-9
canadensis . . .		
brevifolia . . .		
cuspidata . . .		
6 Thujiopsis dolabrata . . .		
7 Cryptomeria japonica . . .	1	25-4
8 Podocarpus macrophylla . . .	1	25-4
9 Taxodium distichum . . .	1	25-9
10 Libocedrus decurrens . . .	1	26-4
11 Thuya gigantea . . .	1	26-4
occidentalis . . .	3	28-2
japonica . . .		
12 Sequoia sempervirens . . .	2	29-7
gigantea . . .		
13 Cupressus Lawsoniana pisifera . . .	9	32-0
obruca . . .		
macrocarpa . . .		
arizonica . . .		
Macnabiana . . .		

[illegible]





[illegible]

APPENDIX B  
RELATIVE VOLUMES OF TRACHEIDS IN TRANSVERSE SECTION, AND THICKNESS OF RADIAL  
WALLS IN THE SPRING AND SUMMER WOODS

	SIZE OF TRACHEIDS IN $\mu$			THICKNESS OF WALLS IN $\mu$		
	Spring Wood T.	Summer Wood T.	Ratio of Volumes	Spring Wood	Summer Wood	Ratio
<i>Dammara australis</i> . . . . .	26.5 x 50	32 x 23	1:1.80	3	5	1:1.66
<i>Araucaria Cunninghamii</i> . . . . .	23.5 x 22.5	23.5 x 22.5	1:1	4.5	4.5	1:1
<i>excelsa</i> . . . . .	27 x 27.5	27.5 x 27	1:1.02	5	5	1:1
<i>Bidwillii</i> . . . . .	16 x 20	13.5 x 18.5	1:1.28	4	4	1:1
<i>Ginkgo biloba</i> . . . . .	35 x 51	35 x 14	1:3.64	3.75	5	1:1.33
<i>Torreya taxifolia</i> . . . . .	36 x 44	40 x 35	1:1.10	2.4	4.8	1:2.00
<i>californica</i> . . . . .	38 x 38	35 x 24	1:1.70	3.6	6	1:1.66
<i>nucifera</i> . . . . .	35 x 44	30 x 25	1:2.05	3.75	8.75	1:2.33
<i>Taxus floridana</i> . . . . .	22 x 31	21 x 17	1:1.90	3.6	4.8	1:1.03
<i>canadensis</i> . . . . .	18 x 19	18 x 17	1:1.10	2.4 } 4.8 }	4.8	1:1.10 } 2 }
<i>brevifolia</i> . . . . .	23 x 33	23 x 20	1:1.60	2.4	4.8	1:2
<i>cuspidata</i> . . . . .	23 x 36.5	20.5 x 20	1:2.07	2.5	4.5	1:1.80
<i>Thujaopsis dolabrata</i> . . . . .	27 x 17	27 x 15	1:1.13	2	5	1:2.50
<i>Cryptomeria japonica</i> . . . . .	27 x 51.5	27.5 x 30	1:1.68	1.5	6	1:4
<i>Podocarpus macrophylla</i> . . . . .	31 x 34	25.5 x 20.5	1:2.01	3.5	5	1:1.43
<i>Taxodium distichum</i> . . . . .	33 x 69	36 x 25	1:2.50	3.6	7.2	1:2
<i>Libocedrus decurrens</i> . . . . .	27 x 30	26 x 12	1:2.60	1.4	2.4 } 4.8 }	1:1.70 } 1:3.43 }
<i>Thuya gigantea</i> . . . . .	26 x 27	29 x 15	1:1.61	1.8	4.8	1:2.66
<i>occidentalis</i> . . . . .	27 x 34	27 x 15	1:2.26	2.1	4.2	1:2
<i>japonica</i> . . . . .	28 x 40	25.5 x 15	1:2.92	1.5	6	1:4
<i>Sequoia sempervirens</i> . . . . .	48 x 62	38 x 24	1:3.26	2.4	7.2	1:3
<i>gigantea</i> . . . . .	33 x 45	42 x 20	1:1.77	2.4	6	1:2.50



## APPENDIX B—Continued

	SIZE OF TRACHEIDS IN $\mu$			THICKNESS OF WALLS IN $\mu$		
	Spring Wood T. R.	Summer Wood T. R.	Ratio of Volumes	Spring Wood	Summer Wood	Ratio
<i>Tsuga Mertensiana</i> . . .	33 × 48	33 × 29	1 : 1.65	2.4	7.2	1 : 3
<i>Pseudotsuga Douglasii</i> . .	30 × 31	27 × 18	1 : 1.91	2.4	7.2 } 9.6 }	1 : 2.91
<i>macrocarpa</i> . . .	31 × 43	29 × 19	1 : 2.41	2.4	7.2	1 : 3
<i>Larix occidentalis</i> . . .	28 × 56	27 × 20	1 : 2.90	2.7	6.4	1 : 2.39
<i>americana</i> . . .	33 × 46	25 × 23	1 : 2.60	2	6	1 : 3
<i>Lyallii</i> . . .	35 × 51	29 × 20	1 : 3.08	1.8 } 4.8 }	8.4	1 : 1.75 } 1 : 4.66 }
<i>leptolepis</i> . . .	35.5 × 50	32 × 22.5	1 : 2.46	2	5	1 : 2.50
<i>Picea Breweriana</i> . . .	29.3 × 36.9	24 × 10.7	1 : 4.10	2.6	5.3	1 : 2
<i>rubra</i> . . .	30.5 × 28.5	30.5 × 15	1 : 1.90	2	4	1 : 2
<i>alba</i> . . .	31 × 36	30 × 22	1 : 1.69	2.4	7.2	1 : 3
<i>Engelmanni</i> . . .	34 × 36	30 × 17	1 : 2.39	2.4	4.8	1 : 2
<i>jescensis</i> . . .	32.5 × 44	32.5 × 20	1 : 2.20	2.5	7.5	1 : 3
<i>polita</i> . . .	38.5 × 47.5	33 × 21.5	1 : 2.57	2.5	6.5	1 : 2.60
<i>bicolor</i> . . .	25.5 × 24	21.5 × 16	1 : 1.72	2.5	4.5	1 : 1.80
<i>pungens</i> . . .	33 × 43	29 × 17	1 : 2.87	1.8	3.6	1 : 2
<i>nigra</i> . . .	32 × 37	32 × 19	1 : 1.94	2.4	5	1 : 2.08
<i>sitchensis</i> . . .	31 × 37	29 × 22	1 : 1.79	2.4	4.8	1 : 2
<i>Pinus Parryana</i> . . .	31 × 33	26 × 19	1 : 2.11	2.4	4.2	1 : 1.75
<i>cembroides</i> . . .	24 × 24	21 × 17	1 : 1.61	2.4	7.2	1 : 3
<i>monophylla</i> . . .	32 × 34	27 × 15	1 : 2.68	2.4	4.2	1 : 1.75
<i>Balfouriana</i> . . .	29 × 35	30 × 17	1 : 1.25	2.4	4.2	1 : 1.75
<i>aristata</i> . . .	26 × 41	26 × 19	1 : 2.16	3	4.2	1 : 1.40
<i>edulis</i> . . .	24 × 25	24 × 12	1 : 2.09	2.4	2.7	1 : 1.12
<i>Lambertiana</i> . . .	40 × 50	36 × 19	1 : 2.92	2.4	4.8	1 : 2
<i>monticola</i> . . .	40 × 46	46 × 27	1 : 1.48	2.4	4.8	1 : 2

<i>Pinus flexilis</i>	32	46	40	25	1:1.47	2.4	3.2	1:1.33
reflexa . . . . .	39	40	33	22	1:2.14	2.4	4.8	1:2
strobilus . . . . .	38	45	34	24	1:2.09	2.4	4.2	1:1.75
parviflora . . . . .	31.5	45.5	32	25	1:1.79	2.4	6	1:2.18
albicaulis . . . . .	31	39	30	22	1:1.83	3.6	4.8	1:1.33
clausa . . . . .	36	60	43	25	1:2.01	3.6	7.2	1:2
rigida . . . . .	30	36	33	21	1:1.56	3	5.5	1:1.83
serotina . . . . .	42	52	46	26	1:1.82	2.4	9.6	1:3
Banksiana . . . . .	34	52	36	21	1:2.33	2.4	6	1:2.50
contorta . . . . .	34	40	31	21	1:2.09	4.2	7.2	1:1.71
glabra . . . . .	34	40	30	29	1:1.56	3.3	4.8	1:1.45
echinata . . . . .	43	53	37	28	1:2.20	2.4	4.8	1:2
resinosa . . . . .	42	54	27	24	1:2.83	3.6	4.8	1:1.33
Thunbergii . . . . .	35	45.5	40	29.3	1:2.14	5.06	8.77	1:1.73
densiflora . . . . .	35	43	32.5	26	1:1.88	2.5	9.5	1:3.80
Murrayana . . . . .	36.5	43	32	19	1:2.57	2.5	7.5	1:3
arizonica . . . . .	32	36	32	21	1:1.71	2.4	3.6	1:1.50
Coulteri . . . . .	35	41	34	23	1:1.83	2.4	4.8	1:2
tuberculata . . . . .	35	44	31	18	1:2.75	3	4.8	1:1.60
Torreyana . . . . .	25	35	25	20	1:1.75	2.4	2.4	1:1
chihuahuana . . . . .	33	44	36	31	1:1.30	2.4	6	1:2.50
Jeffreyi . . . . .	35	42	30	25	1:1.96	3.6	7.2	1:2
ponderosa . . . . .	41	53	35	23	1:2.70	3	4.2	1:1.40
scopulorum . . . . .	28	31	24	22	1:1.64	2.4	7.2	1:3
pungens . . . . .	30	32	31	18	1:1.72	2.4	3.6	1:1.50
inops . . . . .	29	49	26	25	1:2.18	2.4	7.2	1:3
muricata . . . . .	32	40	31	21	1:1.96	2.4	6	1:2
insignis . . . . .	32	39	35	19	1:1.87	3	4.8	1:1.33
Sabiniana . . . . .	35	45	35	26	1:1.73	3.6	4.8	1:1.45
taeda . . . . .	29	50	40	23	1:2.12	3.3	7.2	1:2
palustris . . . . .	42	57	44	27	1:2.01	3.6	4.8	1:2
cubensis . . . . .	45	53	40	29	1:2.05	2.4	4.8	1:2.33
	40	48	38	26	1:1.94	3.9	10.8	1:2.77

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## PLATES



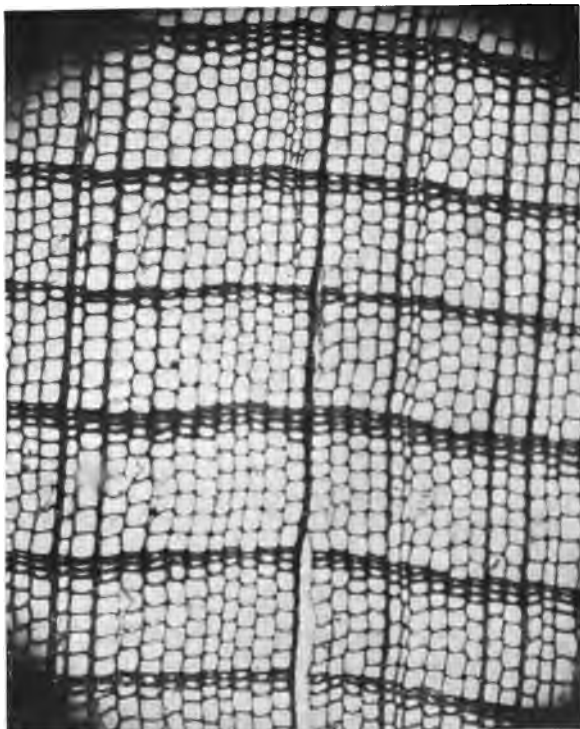


PLATE 1. *PSEUDOTSUGA DOUGLASII*. Transverse section showing the structure of the fine-grained wood.  $\times 41.2$

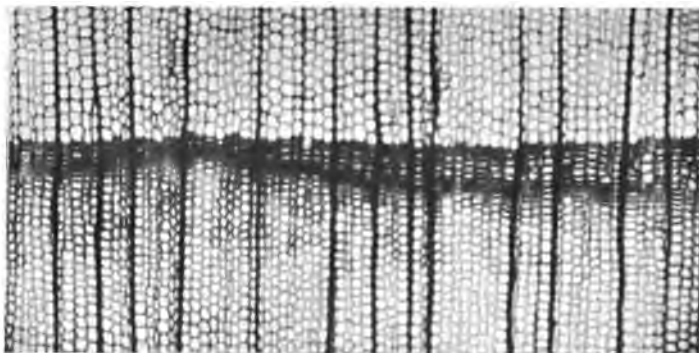


PLATE 2. *TORREYA TAXIFOLIA*. Transverse section showing the coalescence of growth rings in an eccentric development.  $\times 51$



PLATE 3. *CORDAITES BRANDLINGII*. Radial section of the transition zone next to the pith, showing the protoxylem to be wholly composed of spiral tracheids.  $\times 153.4$



PLATE 4. *CORDAITES BRANDLINGII*. Radial section of the transition zone immediately external to the preceding, and showing the spirals of the tracheids passing into scalariform structure.  $\times 153.4$



PLATE 5. *CORDAITES BRANDLINGII*. Radial section immediately external to fig. 4, showing the complete formation of scalariform structure.  $\times 153.4$



PLATE 6. *CORDAITES BRANDLINGII*. Radial section immediately external to fig. 5, showing the reduction of the scalariform structure into imperfectly formed, multiseriate, bordered pits.  $\times 153.4$



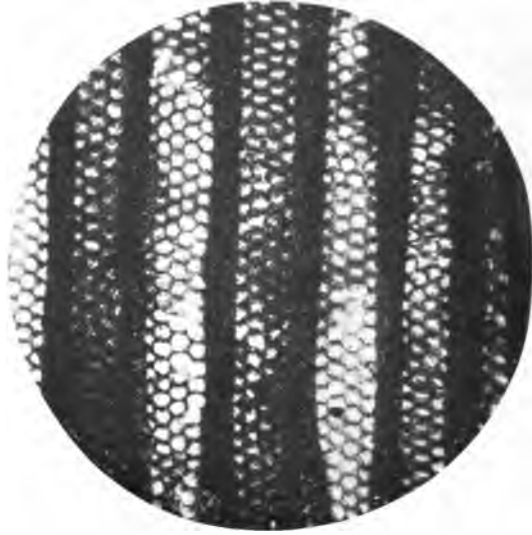


PLATE 7. *CORDAITES ACADIANUM*. Radial section showing the completed bordered pits with a primitive arrangement.  $\times 180$



PLATE 8. *CORDAITES NEWBERRYI*. Radial section showing the peculiar grouping of the bordered pits.  $\times 180$



PLATE 9. *CUPRESSUS NOOTKATENSIS*. Radial section showing the longitudinal distribution of fungus mycelia in the tracheids of the wood.  $\times 150$

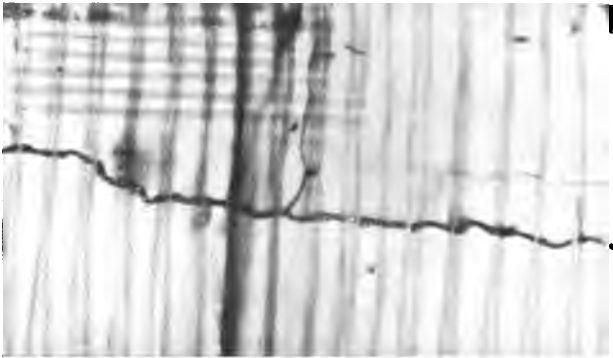


PLATE 10. *CUPRESSUS NOOTKATENSIS*. Radial section showing the transverse distribution of fungus mycelia in the tracheids of the wood, and their relations to the tracheid walls.  $\times 150$



PLATE 11. *PSEUDOTSUGA MIOCENA*. Radial section showing the effects of decay in breaking up the substance of the cell wall along the lines of striation.  $\times 127.8$

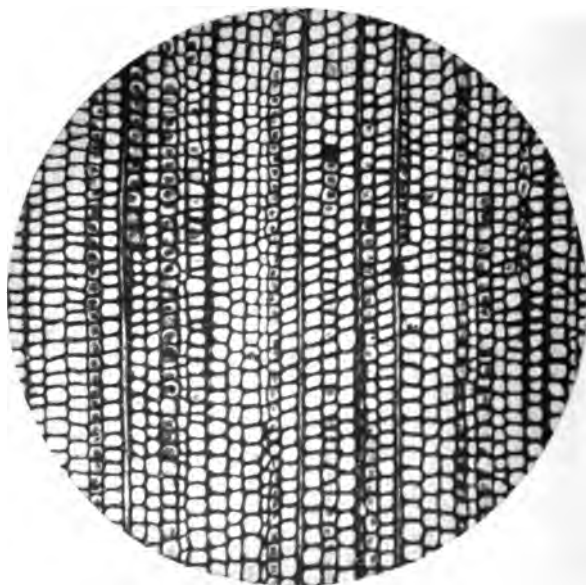


PLATE 12. *CORDAITES MATERIARIUM*. Transverse section showing the absence of growth rings, the character of the tracheids, and the distribution of resinous tracheids near the medullary rays.  $\times 40.9$

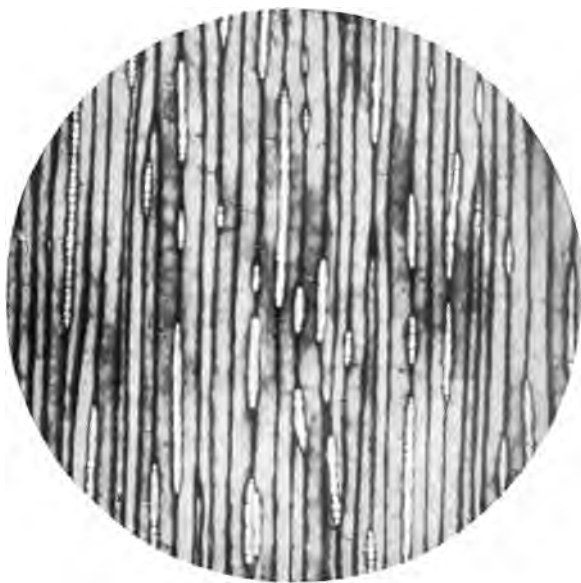


PLATE 13. *CORDAITES MATERIARIUM*. Tangential section showing the character of the ordinary medullary rays which are sometimes two-seriate.  $\times 40.9$

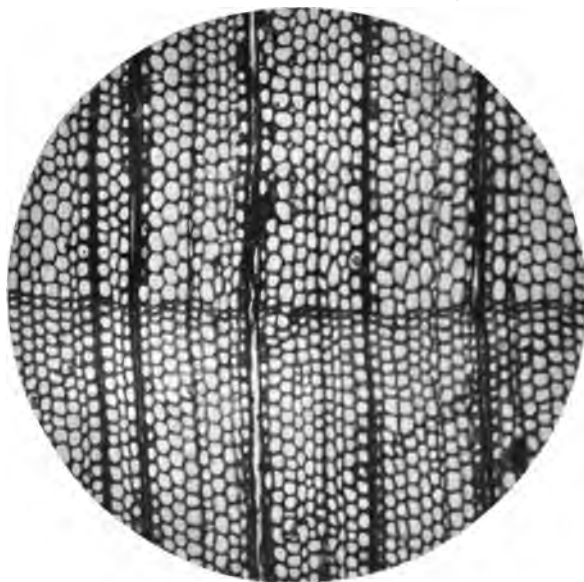


PLATE 14. *DAMMARA AUSTRALIS*. Transverse section showing the clearly defined growth ring and its summer wood, and the distribution of resin cells near the medullary rays.  $\times 46.8$



PLATE 15. *DAMMARA AUSTRALIS*. Tangential section showing the character of the medullary rays and the occurrence and location of plates of resin.  $\times 52$

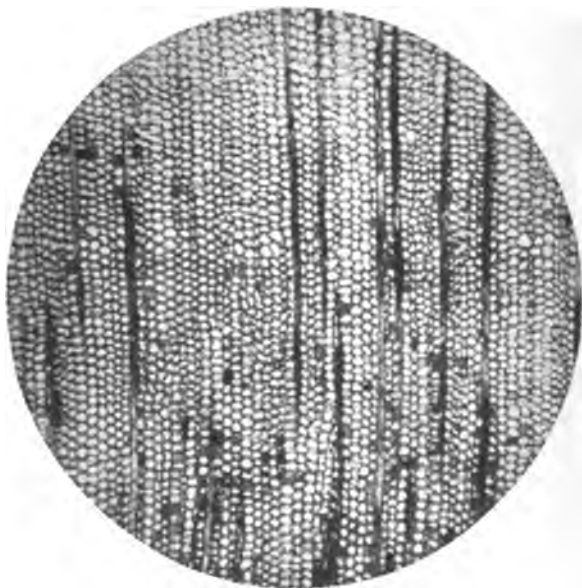


PLATE 16. *ARAUCARIA GLAUCA*. Transverse section showing the general character of the structure, the absence of growth rings, and the distribution of resinous tracheids.  $\times 46.8$



PLATE 17. *ARAUCARIA GLAUCA*. Tangential section showing the character of the medullary rays.  $\times 46.8$

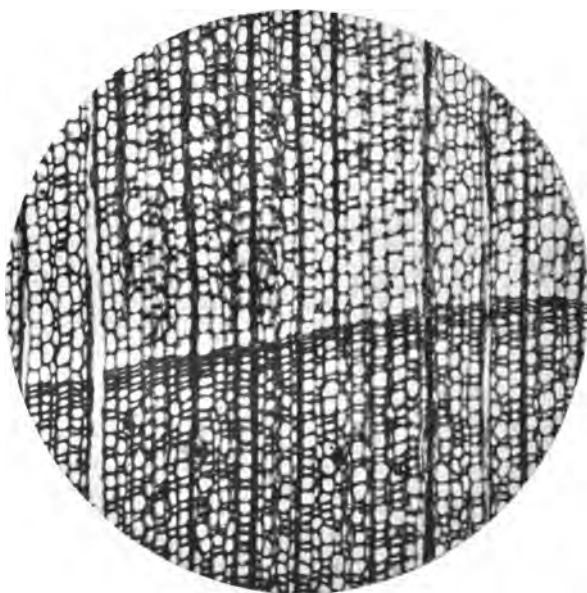


PLATE 18. *GINGKO BILOBA*. Transverse section showing the development of a strong growth ring, and the occurrence of crystals as indicated by dark spots in line with the tracheids.  $\times 46.8$



PLATE 19. *GINGKO BILOBA*. Tangential section showing the character of the very low medullary rays.  $\times 52$

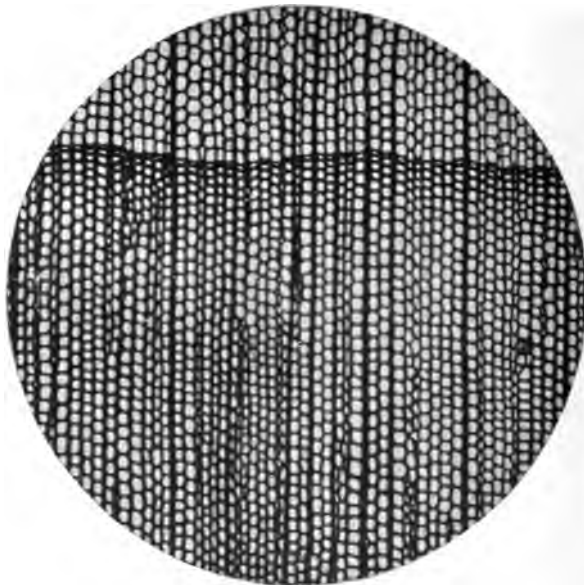


PLATE 20. *TORREYA TAXIFOLIA*. Transverse section showing the very thin and open summer wood.  $\times 46.8$



PLATE 21. *TORREYA TAXIFOLIA*. Tangential section showing the character of the medullary rays.  $\times 52$

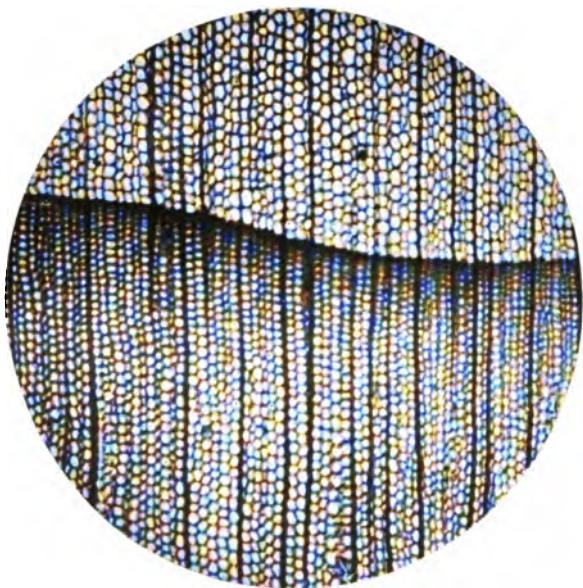


PLATE 22. *TAXUS CUSPIDATA*. Transverse section showing the rather dense structure of the thin summer wood.  $\times 46.8$





PLATE 31. *TAXODIUM DISTICHUM*. Tangential section showing the character of the medullary rays.  $\times 46.8$

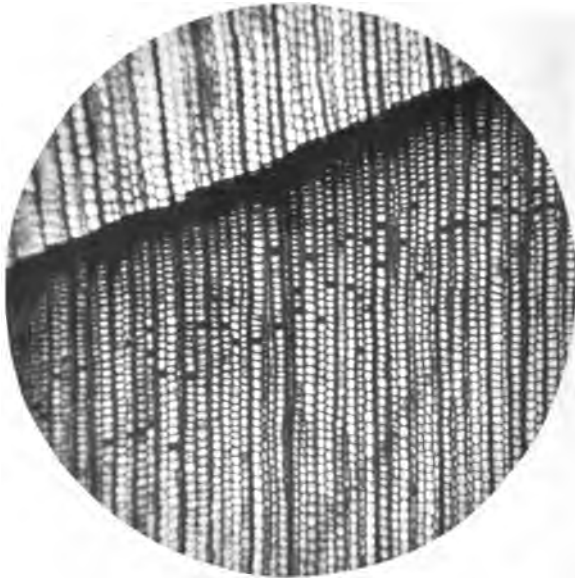


PLATE 32. *LIBOCEDRUS DECURRENS*. Transverse section showing the dense summer wood and the distribution of the resin cells.  $\times 46.8$



PLATE 33. *LIBOCEDRUS DECURRENS*. Tangential section showing the character of the rather broad medullary rays and the occurrence of resin.  $\times 64$

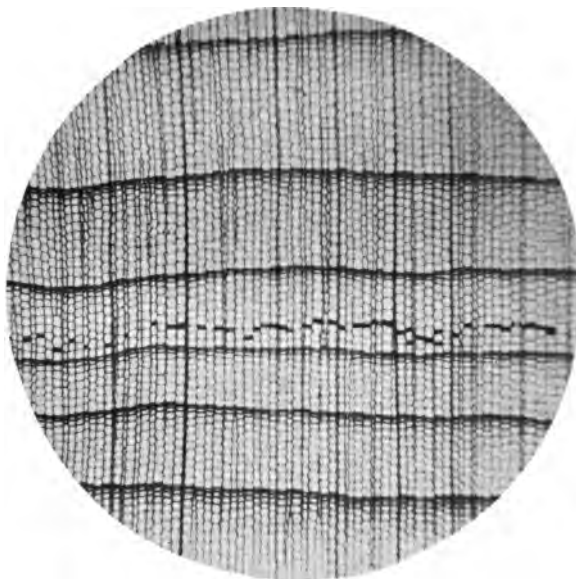


PLATE 34. *THUYA OCCIDENTALIS*. Transverse section showing the narrow growth rings, the very thin summer wood, and the distribution of the resin cells.  $\times 46.8$



PLATE 35. *THUYA OCCIDENTALIS*. Tangential section showing the very narrow medullary rays with narrowly oblong cells, taken from the spring wood.  $\times 64$

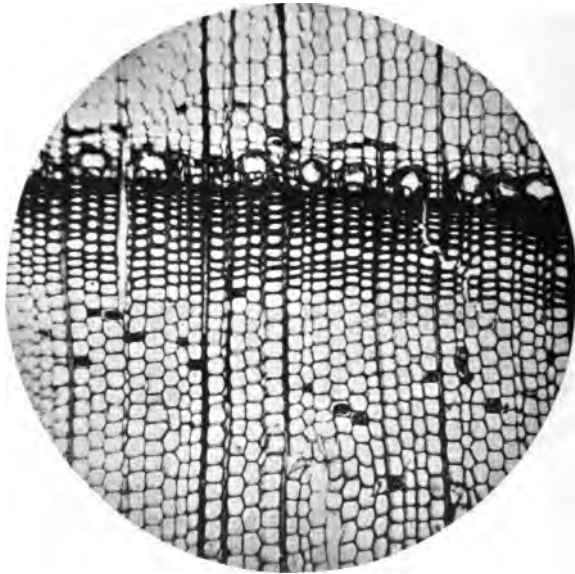


PLATE 36. *SEQUOIA SEMPERVIRENS*. Transverse section showing the very large tracheids of the spring wood with thin walls, the rather dense summer wood with a somewhat abrupt transition from the spring wood, the scattering distribution of the resin cells, and the occurrence of resin sacs in the initial layer of the spring wood.  $\times 46.8$



PLATE 37. *SEQUOIA SEMPERVIRENS*. Tangential section from the spring wood showing the very broad medullary rays, the cells of which are equal and uniform.  $\times 64$

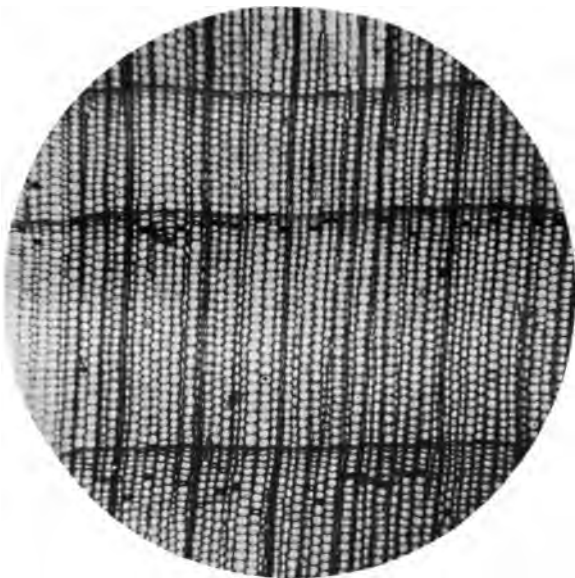


PLATE 38. *CUPRESSUS GOVENIANA*. Transverse section showing the very thin summer wood and the distribution of the resin cells.  $\times 46.8$

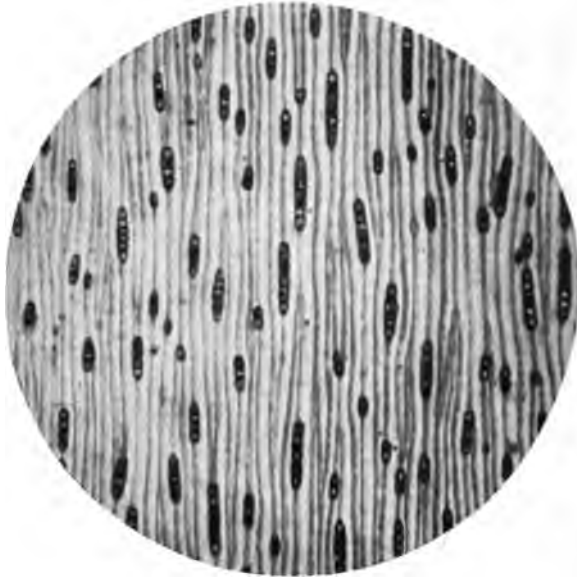


PLATE 39. *CUPRESSUS GOVENIANA*. Tangential section showing the very broad and low medullary rays.  $\times 52$

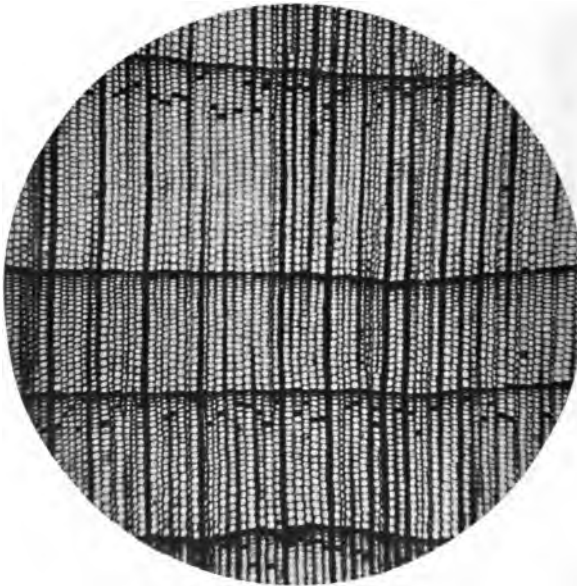


PLATE 40. *JUNIPERUS CALIFORNICA*. Transverse section showing the character of the growth rings and the distribution of the resin cells.  $\times 46.8$

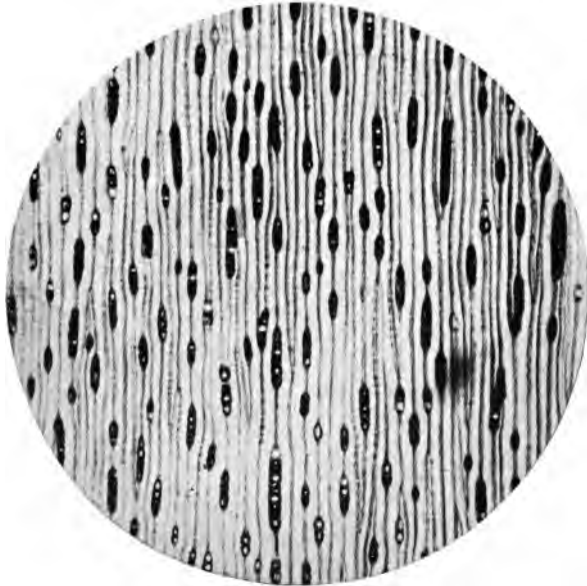


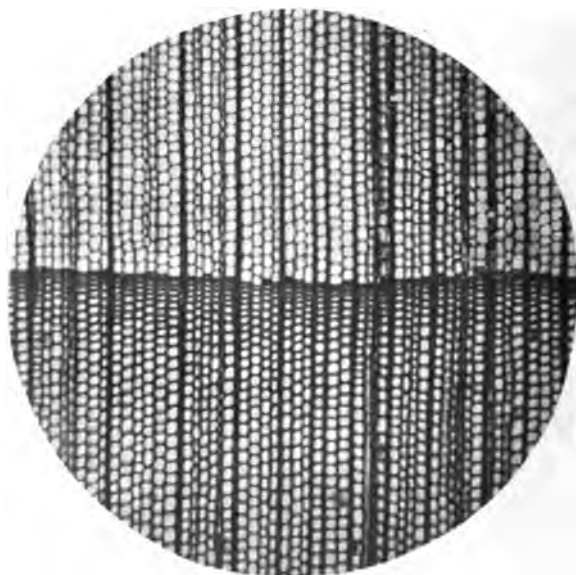
PLATE 41. *JUNIPERUS CALIFORNICA*. Tangential section through the spring wood showing the character of the low medullary rays.  $\times 64.8$



PLATE 42. *ABIES NOBILIS*. Transverse section showing the occurrence of resin canals and the distribution of scattering resin cells on the outer face of the summer wood.  $\times 39.2$



**PLATE 43; ABIES NOBILIS.** Tangential section showing the character of the medullary rays.  $\times 46.8$



**PLATE 44. TSUGA PATTONIANA.** Transverse section showing the character of the summer wood and the distribution of the resin cells on the outer face of the growth ring.  $\times 46.8$



PLATE 45. *TSUGA PATTONIANA*. Tangential section through the spring wood showing the character of the medullary rays.  $\times 46.8$

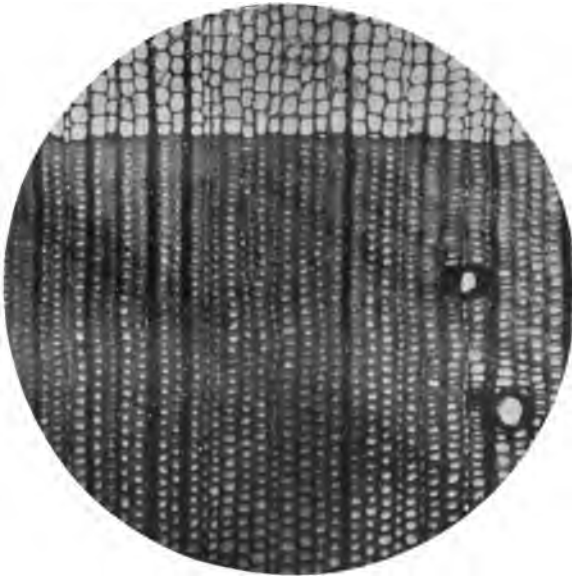
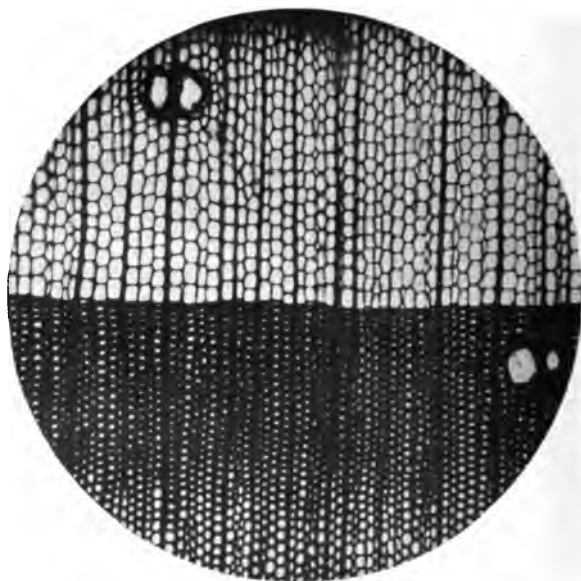


PLATE 46. *PSEUDOTSUGA DOUGLASII*. Transverse section showing the broad and dense summer wood in a coarse-grained form, and the distribution of the resin canals.  $\times 46.8$





**PLATE 47. *PSEUDOTSUGA DOUGLASII*.** Tangential section showing the low and broad ordinary rays, together with the often very unequal and narrow fusiform rays.  $\times 46.8$



**PLATE 48. *LARIX AMERICANA*.** Transverse section showing the dense and broad summer wood and the distribution of resin canals.  $\times 46.8$

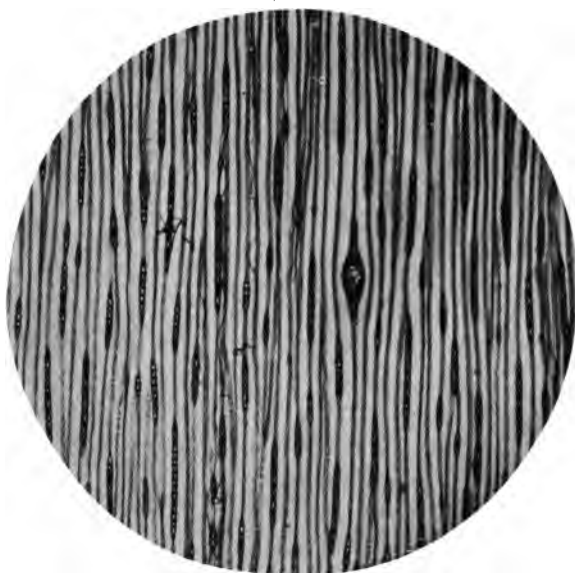


PLATE 49. *LARIX AMERICANA*. Tangential section from the spring wood showing the narrow ordinary rays and the rather broad fusiform rays.  $\times 46.8$

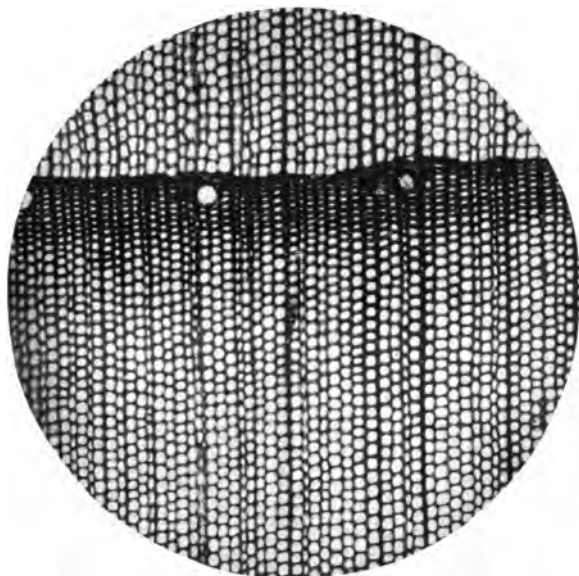


PLATE 50. *PICEA NIGRA*. Transverse section showing the character of the general structure and the distribution of the resin canals.  $\times 46.8$



PLATE 51. *PICEA NIGRA*. Tangential section through the spring wood showing the structure of the two forms of medullary rays.  $\times 46.8$

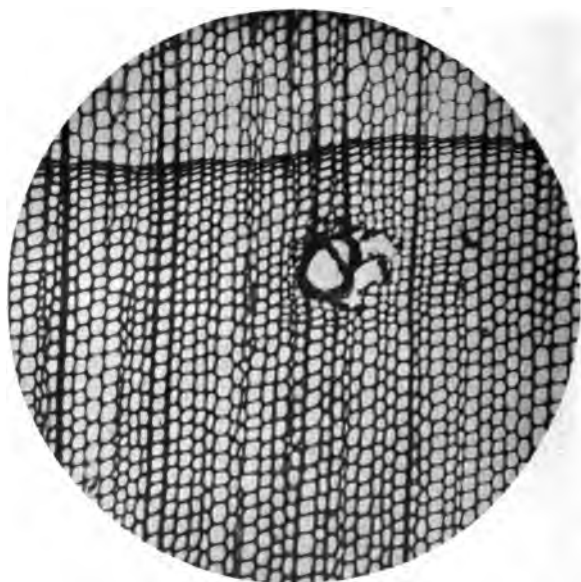


PLATE 52. *PINUS MONTICOLA*. (Type of soft pines, Sec. I.) Transverse section showing the large and thin-walled tracheids of the spring wood, the very thin and open summer wood, the large resin canals with the associated parenchyma broken out.  $\times 46.8$



PLATE 53. *PINUS MONTICOLA*. Tangential section showing the structure of the two forms of medullary rays.  $\times 46.8$

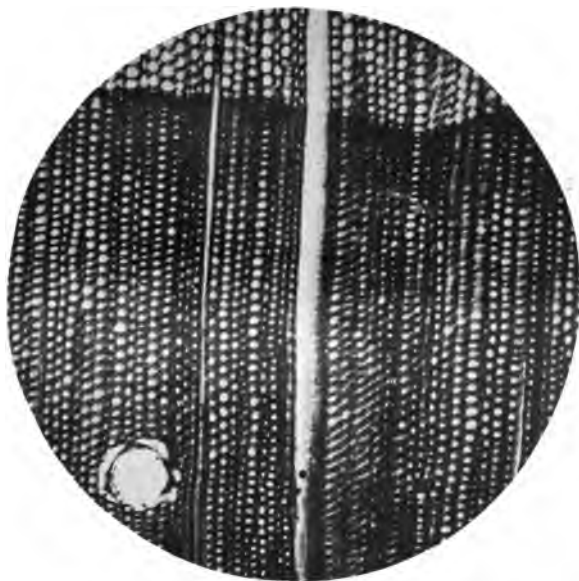


PLATE 54. *PINUS GLABRA*. (Type of hard pines, Sec. II.) Transverse section showing the very broad and very dense summer wood, and the structure of a resin canal with very large epithelial cells.  $\times 46.8$



**PLATE 55. PINUS GLABRA.** Tangential section through the spring wood showing the ordinary rays with terminal tracheids and with the thin-walled parenchyma all broken out; the interspersal of the tracheids and their general predominance; the structure of the low and rather broad fusiform ray, the thin-walled parenchyma cells of which have been broken out, leaving only a portion of the resin canal in the central tract together with the terminal tracheids.  $\times 46.8$





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